

8-2016

Population Dynamics of Black Bears in Northwestern South Carolina

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POPULATION DYNAMICS OF BLACK BEARS
IN NORTHWESTERN SOUTH CAROLINA

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Wildlife and Fisheries Biology

by
Shefali Azad
August 2016

Accepted by:
Dr. David Jachowski, Committee Chair
Dr. Patrick Jodice, Committee Co-Chair
Dr. Yoichiro Kanno

ABSTRACT

Black bears (*Ursus americanus*) are managed as a game species in the northwestern region of South Carolina. However, no formal research study has examined their long-term population trends. I used the Downing harvest population reconstruction technique to establish abundance trends. The total population in 2013 was estimated at about 412 bears, increasing from about 97 bears in 1998. I also derived abundance, density, average age, and sex ratios at a county-level to investigate differential stages of recovery. Overall my results suggest that in 1998-2013 Oconee county had a rapidly expanding population, Pickens county requires further investigation into potential bear overharvest, and the Greenville county population is dispersing from Wildlife Management Areas to private lands. My findings suggest that further research into predictive models to determine the maximum sustainable harvest rate for this population and quantify management decisions is needed.

I also analyzed black bear capture-recapture data collected by the South Carolina Department of Natural Resources (SCDNR) using hair snares in 2013-2014, to estimate density. I compared results from non-spatial and spatially explicit models. Black bear density estimated from non-spatial models was 0.187 bears/km² (SE=0.071 bears/km²) in 2013 and 0.156 bears/km² (SE=0.056 bears/km²) in 2014. Density estimated from spatially explicit models was 0.168 bears/km² (SE=0.024 bears/km²) in 2013 and 0.177 bears/km² (SE=0.023 bears/km²) in 2014. Non-spatial methods showed greater variance between models, and suggest violation of geographic closure assumptions. Overall I recommend that spatial models be used in future capture-recapture surveys to establish

density and sex ratios.

Finally, I undertook a preliminary investigation into the usefulness of acorn mast, human-bear interactions, and bait station visitation indices collected by the SCDNR. I found that the quality of white, red, and chestnut oak acorn crops significantly predicted black bear population growth rates (λ). My results also suggested that bears avoid the human-dominated landscape in plentiful acorn years. Bait station indices did not significantly predict λ , and I recommend a focused study into the viability of increasing resources to improve the statistical power of these surveys.

DEDICATION

This work is dedicated to the memory of Dr. Kate McFadden, who threw caution to the wind and took on a student she had never seen or spoken to, and who was embarrassingly new to the field. Thank you, Kate.

ACKNOWLEDGMENTS

I would like to first and foremost thank my advisor, Dr. David Jachowski, for his unfailing support and guidance throughout this endeavor, for setting me on a path of thinking like an ecologist, and for helping me become a better writer in the process. I also thank my committee members, Dr. Patrick Jodice and Dr. Yoichiro Kanno, for their scientific comments and suggestions on my research. I would like to acknowledge the South Carolina Department of Natural Resources (SCDNR), in collaboration with the USGS South Carolina Cooperative Fish and Wildlife Research Unit, for their funding and support on this project. My especial thanks to Tammy Wactor, my collaborator at the SCDNR, for the countless hours spent looking up old datasets and talking me through my results in the context of bear management in South Carolina. I am also highly indebted to all the field technicians at SCDNR over the years that collected the data used in this study. My gratitude also goes out to Dr. Joseph Clark at the USGS Southern Appalachian Research Branch, and Dr. William Bridges and Dr. Colin Gallagher over at the Department of Mathematical Sciences, for all their statistical expertise and advice, and without whom I would still be pulling my hair out trying to analyze my data.

I would like to thank my parents, for their unconditional love and support in every life decision I have ever made, and for tirelessly encouraging me every time I faltered along this journey. Finally, to my sister, my graduate colleagues, and more friends than I could possibly list, my eternal gratitude for the patient ear to my vents, the welcome comedic distractions, and the words of wisdom that got me through these past two years and undoubtedly many more to come.

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CHAPTER ONE

DEMOGRAPHIC TRENDS OF A HARVESTED BLACK BEAR POPULATION IN NORTHWESTERN SOUTH CAROLINA

INTRODUCTION

Attitudes towards carnivores in North America have changed substantially over time; from persecution in the times of European immigrant settlements (Taber and Payne 2003), to a gradual shift towards protection, beginning with the era of wildlife management in the early 20th century (Miller et al. 2013). More recently, since the 1980s, factors such as habitat expansion through abandonment of small farm holdings, removal of bounties, listing of threatened species, and harvest age/sex/bag regulations have led to persistence as well as, in some cases, expansion of large-carnivore populations (Maehr et al. 2001, Hristienko and McDonald 2007, Miller et al. 2013). A leading example has been the recovery of black bear (*Ursus americanus*) in the eastern United States, with overall populations reportedly growing by 13% from 1970 to late-1980s (Cowan 1972, Garshelis and Hristienko 2006). Currently the black bear is estimated to occupy 62% of its historic range in North America (Pelton and van Manen 1994), and 31 of 33 U.S. states with a resident black bear population report either stable (3 of 31) or increasing (28 of 31) abundance from 1988-2001 (Hristienko and McDonald 2007, Noyce 2011b).

With black bear populations increasing over much of their range, the focus of management has shifted in many states from restoration to managing human-animal interactions (Organ and Ellingwood 2000). Human-animal interactions include not only

threats to life and property, but also opportunities for recreational hunting. Management plans for black bear vary with geography and distribution; and whether it is a nuisance population, one maintained for harvest, or one conserved for viewing and demographic stability (Bowman et al. 2001, VDGIF 2002). Most management strategies deal with harvest regulations, ranging from restrictions on bag limits and duration of hunting season, to full legal protection in some smaller refuges or parks (e.g., Nantahala National Forest, Great Smoky Mountains National Park). However, in order to develop adaptive management strategies that reconcile recovering or expanding bear populations with increasing human densities, it is important to first understand how harvest regulations impact populations.

In South Carolina, according to historical accounts (Ramsay 1809:305), black bears once roamed throughout the land, and were so numerous, at this period [1750] in the upper-country, that “a common hunter could kill in the autumnal season as many bears as would make from two to three thousand weight of bear bacon.” By 1859, Logan declared from pelt records and local lore that the black bear was probably extinct in the region, from a combination of inhabitation and cultivation of land, and hunting for meat and sport by the English (Logan 1859). Over a century later, Cely and Hamilton (1981) reported a “guestimate” of the South Carolina population at several dozen, warning that rapid urban development was fragmenting bear habitat. Currently, South Carolina possesses two distinct resident black bear populations - in the northwest mountainous region (legally hunted since 1981), and in the eastern upper coastal plain (legally hunted since 2011). Annual status reports estimated a stable northwest population at ~90-100

bears from 1989 to 1992, and overall population of ~175-200 bears in 1994 (Fendley 1991, Stokes 1992, Stokes 1994). In 2003, based on results from a multi-state study (Settlage 2005), the northwest population was estimated at 300-450 bears (Skip Still, SCDNR, pers. comm.). Annual status reports in 2007 and 2011 reported a statewide population of ~1,150 and ~1800 bears respectively (Still 2007, Morton 2011), from personal observations by state wildlife personnel of increasing harvest numbers, bear sightings, and bear-human conflict. However no formal research study had verified this estimate. Thus there was a need for estimating the abundance and population dynamics of black bears, and surmising the impact of harvest on population trends, such that appropriate regulations might be recommended for recreational hunting in order to maintain desired population levels or trends.

I sought to assess the long-term progression and current state of black bear recovery in the northwest region of South Carolina, at both regional and county levels. I selected a longstanding hunting dataset to perform the population reconstruction. Population reconstruction techniques are deterministic models that estimate a minimum abundance from age- and sex- specific harvest data by carrying out a backward addition of cohorts. From a managerial standpoint, I also sought to ascertain whether the population growth rates were sustainable given harvest practices in the state.

METHODS

Study Area

I defined the study area as the region where hunting of bears was permitted in northwest South Carolina. The South Carolina Department of Natural Resources (SCDNR) characterized this region as ‘Game Zone 1’, and it extended over the counties of Oconee, Pickens, and Greenville (Figure 1.1). Forest types in the northwest region of South Carolina generally consisted of shortleaf pine (*Pinus echinata*), chestnut oak (*Quercus prinus*) and scarlet oak (*Q. coccinea*) mixes on the southern Appalachian slopes (Willey 1995, Butfiloski 1996). The cooler northern slopes consisted of yellow poplar (*Liriodendron tulipifera*), white pine (*P. strobus*), eastern hemlock (*Tsuga Canadensis*), and mixed mesophytic hardwood overstories (Willey 1995, Butfiloski 1996). Slopes and coves often had dense understories of mountain laurel (*Kalmia latifolia*) and rhododendron (*Rhododendron maximum*), and intermediate stands were generally oak-pine mixtures (Myers et al. 1986). The study area was generally characterized by a mean annual temperature of 15.5 °C and mean annual precipitation of 160 cm over the study period considered (1998-2015; NOAA 2015).

Previous black bear studies in the region (Fendley 1991, Willey 1995) indicated that populations of black bear were concentrated to the forests to the east of Jocassee lake (Pickens and Greenville counties) and that hunting effort was relatively lower (~11% of all harvest in 1981-1991) in Oconee county, yet Oconee reported approximately 33% of total bear harvests (SE=0.088) in 1992-2015 (Figure 1.2). Further, different counties exhibited different trends in which sex of bears were harvested. For example, Pickens

county consistently reported a higher female bias in harvest than Oconee and Greenville (Table 1.2). Therefore, I decided to reconstruct populations at both the region and county level.

Although harvest records were available for both public and private lands combined, I did not have an estimate of area for private hunting grounds. Therefore, while I estimated abundance for the entire northwest region, I defined separately a subset of public state WMA lands (both owned and leased by SCDNR), for the purposes of estimating density (Figure 1.1). The SCDNR allotted the following acreage of WMA lands for bear hunting in each county: Pickens = 156.3 km², Oconee = 345.6 km², and Greenville = 36.4 km² (Tammy Wactor, SCDNR, pers. comm.). I defined the total public lands available over the northwest region as the summation of county WMAs = 538.3 km².

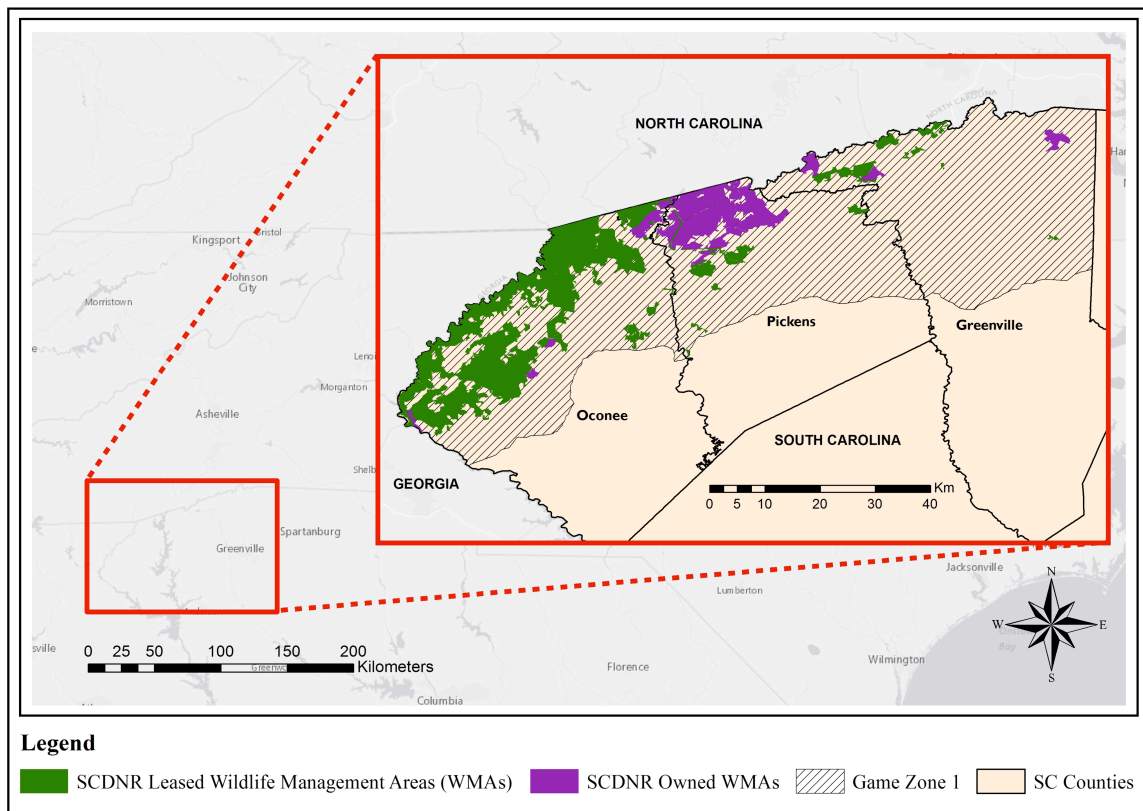


Figure 1.1. Location of the South Carolina Department of Natural Resources defined Game Zone 1 for black bear harvest in the northwest region, and Wildlife Management Area lands in the Zone.

Data collection

I used 18 years of annual harvest records (1998-2015) maintained by the SCDNR to reconstruct black bear populations in northwest South Carolina. In South Carolina, bear hunts were undertaken annually in two forms - still hunts (bears stalked and shot by single hunter) and party dog hunts (bears run down by pack of dogs and multiple hunters). The season for still hunts consistently ran between October 17-23 during the study period (S.C. Code Ann. § 50-11-430; T. Wactor, pers. comm.). The limits on each hunter (consistent through the dataset period) were 1 bear per hunting season, no sow with cubs, no bears 45 kg or less. The season for party dog hunts ran between October 24-30. The limit on each party (of up to 25 hunters) was 5 bears per hunting season, no sow with cubs, no bears 45 kg or less (S.C. Code Ann. § 50-11-430). South Carolina DNR personnel recorded the sex and location of kill for each harvest reported, and collected a tooth for age analysis using the cementum annuli technique (Wiley 1974). However, as tooth analysis was carried out beginning 1992, age estimates were only available for 1992 onwards. While harvest numbers varied considerably each year, I noted that prior to the mid-90s, bear harvest was generally ≤ 10 bears/year (Figure 1.2). Thereafter, harvest levels increased, to as high as 127 in 2013 (Figure 1.2).

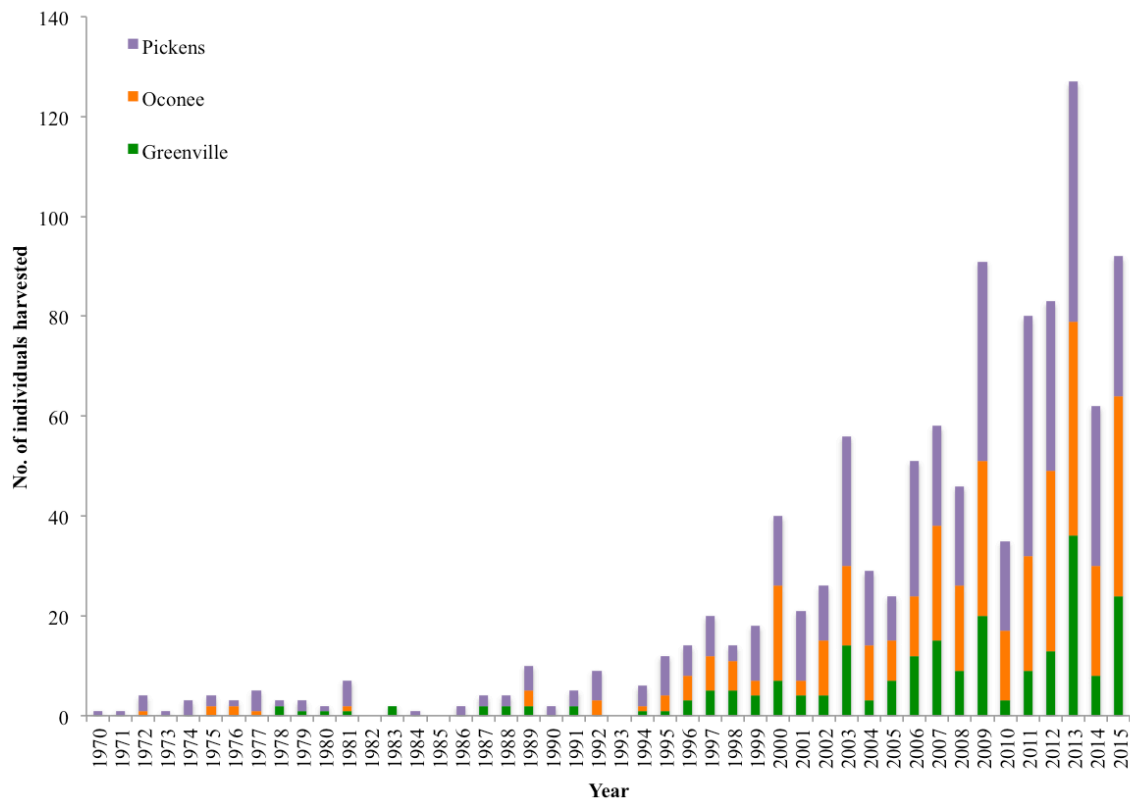


Figure 1.2. Overall black bear harvest (# of individuals) by county in Pickens, Oconee, and Greenville counties of Game Zone 1, northwest South Carolina, 1970-2015.

Model selection

I used a Downing (1980) adaptation of the Virtual Population Analysis (VPA) developed by Fry (1949) to reconstruct the northwest South Carolina black bear population through backwards summation of cohorts. This technique is suitable for analysis of age- and sex- specific harvest data that are typically collected by managers (Warburton 1996, Bender 1997, Jones 2005, Noyce 2011b). Unlike later adaptations of the harvest reconstruction technique (e.g., Creed et al. 1984, Fryxell et al. 1988, Roseberry and Woolf 1991) the Downing model does not require additional inputs of hunting effort, reporting rate or recruitment/survival vectors to calibrate the model (all of which were unavailable for my dataset). The method also allowed for the collapsing of the older age classes. This was useful for a long-lived species such as the black bear, as it decreased the time taken for a cohort to pass through the population and be accounted for in the reconstruction. Finally, evaluation and limitations of the Downing method had been documented in the literature and could serve as a guide in reporting population estimates (Tilton 2005, Davis et al. 2007, Klopfer 2011).

While I determined that the Downing method was the most appropriate method for my analysis, there were some important assumptions of this technique to consider. First, similar to other hunted bear populations; I assumed that the primary source of mortality for the population was harvest based (Wooding and Hardisky 1994, Klenzendorf 2002). However, to help account for a likely secondary source of mortality, I augmented my data by including roadkill mortalities in the harvest. Second, I assumed harvest of black bear was non-differential towards age or sex, for all age classes ≥ 1 (cubs

< 1 year were not allowed to be harvested). Third, I assumed due to non-differential harvest that the two oldest age classes of the population had equal mortality rates, with the ratio of harvest to non-harvest mortality constant over time. Since a varying number of bears each year were reported as un-aged, I improved robustness by inflating harvest records by a factor equal to the proportion of un-aged bears in the dataset for that year (Davis et al. 2007).

Reconstruction technique

I applied the Downing technique to a subset of the harvest database, from 1998-2015. Prior to 1992, tooth-aging data, and thus age-specific harvest, were unavailable. In both 1993 and 1997, no harvest occurred, and I could not apply the Downing equations to those years. I implemented the Downing technique by first collapsing harvest records for older age classes into a single age class. I calculated an “average harvest” (H) and “average mortality rate” (M) for the two oldest age classes over the last three years, and divided H by M to derive a “starting abundance” (A). I used A along with the ratio of actual harvest to H to derive abundances for the two oldest age classes. I estimated abundance over all other age classes by backwards summation (Appendix A).

I ran reconstruction models on 7 datasets, derived by collapsing age classes to 3+, 4+, 5+, 6+, 7+, 8+, and 9+ years. However I only reported abundance from models for 3+, 4+, and 5+ collapses, as I observed that harvest counts were sparser for older age classes leading to incomplete cohort construction and computational biases in the models when I collapsed age classes >6 years. Because reconstruction is complete when a cohort

passes through the harvested population, collapsing to $n+$ age classes allowed a complete reconstruction up to the $(n - 1)$ th year prior to present. Accordingly, collapsing to 3+ - 5+ age classes is a standard protocol in the estimation of black bear abundance by wildlife managers using the Downing technique (Tilton 2005, Klopfer 2011, Noyce 2011a). It should be noted that the Downing technique provides a yearly point estimate of abundance with no method for calculating variance within a year. Therefore, I reported mean of abundance estimates from the 3 collapse models, but no estimate of variance around the mean.

I estimated abundance using all harvest records (on both public as well as private lands). I derived density estimates from a subset of the records reporting harvest from WMA lands only. Finally, I derived estimates separately for all 3 counties as well as over the entire northwest population. For the entire northwest SC population I established abundance trends, derived density, population growth rate, and age-specific survival. At a county level I established abundance trends, derived density, population growth rate, average age of bears, and percentage male/female in harvest. Note that since I collapsed higher age classes, oldest age classes were not the true oldest age classes; thus survival estimates for later years increased to > 1.0 and were removed from the results (Table 1.1).

RESULTS

Demographics of the entire northwest population

I estimated that abundance had been generally increasing in the entire northwest (including both public and private hunting lands) over the study period, jumping from a

mean (average of the values of the 3+, 4+, and 5+ age collapse models) of 96.7 bears in 1998 to 412.0 bears in 2013 (Figure 1.3). I derived density estimates over public lands using the WMA geographic extent of 538.3 km², which showed a correspondingly increasing trend, from 0.158 bears/km² in 1998 to 0.452 bears/km² in 2013 (Figure 1.4). Mean population growth rate was 1.111 per year (SE=0.128). With the exception of 2000, 2003 and 2012, population growth rate averaged over models was > 1.0 for every year since 1998. I noted that there was no significant difference ($P > 0.878$) between Downing abundance estimates for public + private lands collectively, and Downing abundance estimates for only public lands inflated by the ratio of WMA harvests to collective harvest.

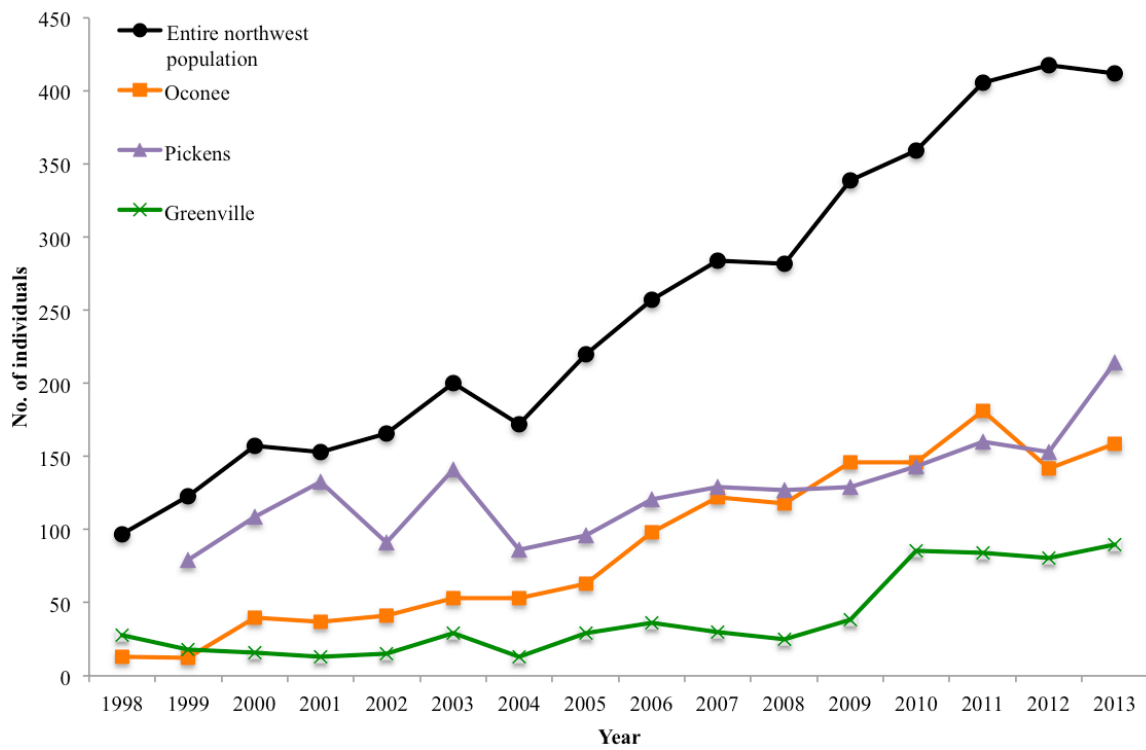


Figure 1.3. Model averaged abundance (# of individuals) trends of the black bear population of northwest South Carolina, estimated over both private and public (Wildlife Management Area) lands, in 1998-2013.

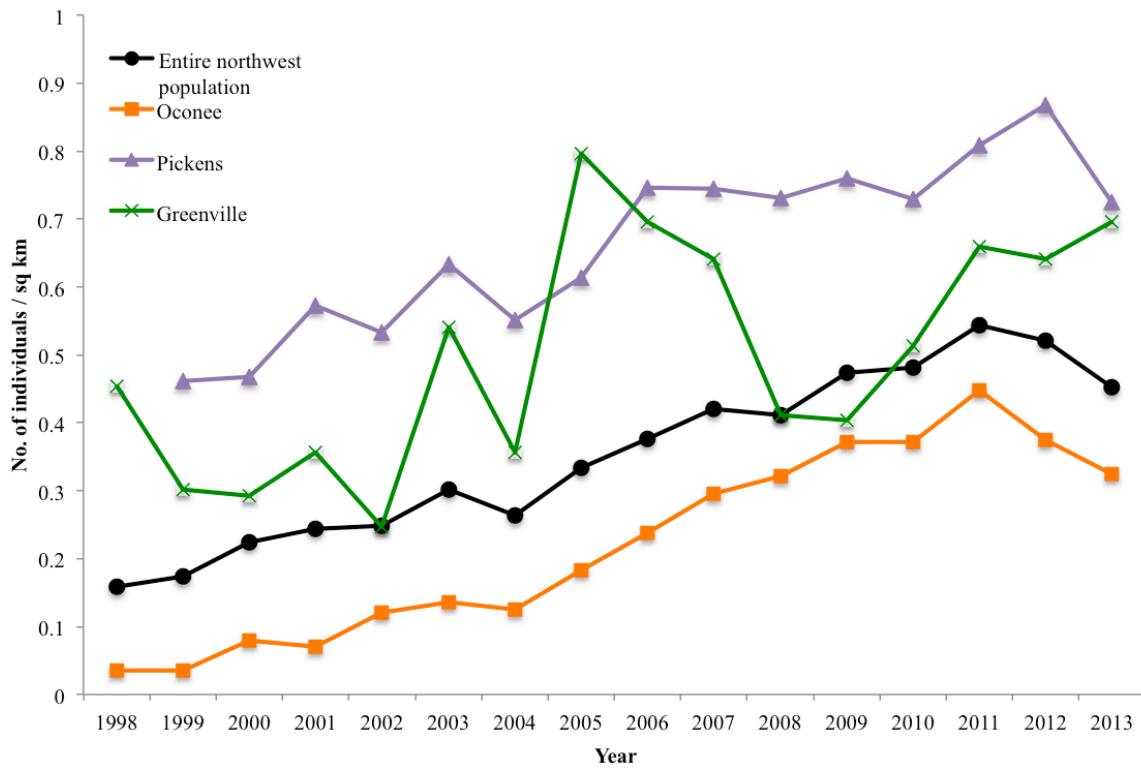


Figure 1.4. Model averaged density (# of individuals/km²) trends of the black bear population of northwest South Carolina, estimated over public (Wildlife Management Area) lands, in 1998-2013.

Mean annual survival ranged from 0.684 to 0.843 depending on the age class (Table 1.1). There was no significant variance in survival across models of different collapses ($P > 0.25$ for all age classes) (Table 1.1), suggesting that the Downing method was robust to survival estimates within an age class. Excluding the oldest age class 7 (biased due to collapse of older age classes), I noted that age class 1 reported highest survivorship rates across all collapse models, and even age classes (2, 4, 6) consistently reported lower mean survivorship than odd age classes (3, 5) across all collapse models (Table 1.1).

Table 1.1. Age-specific survival of black bear, reported as mean and standard error (SE) for each model in 1998-2013, and p-value for analysis of variance between models, for the northwest population of South Carolina, USA.

Model	Age Class						
	1	2	3	4	5	6	7
	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Collapse to 9+	0.786 (0.125)	0.712 (0.170)	0.771 (0.142)	0.717 (0.296)	0.715 (0.107)	0.696 (0.174)	0.843 (0.99)
Collapse to 8+	0.797 (0.117)	0.723 (0.178)	0.781 (0.135)	0.734 (0.213)	0.738 (0.146)	0.684 (0.208)	
Collapse to 7+	0.785 (0.127)	0.692 (0.180)	0.743 (0.179)	0.696 (0.267)	0.795 (0.077)		
Collapse to 6+	0.807 (0.129)	0.744 (0.173)	0.805 (0.132)	0.781 (0.163)			
Collapse to 5+	0.801 (0.103)	0.703 (0.218)	0.716 (0.296)				
Collapse to 4+	0.806 (0.124)	0.739 (0.184)					
p-value	0.99	0.96	0.71	0.78	0.24	0.9	--

Demographics at a county level

Oconee county. — In Oconee county, I found that public harvest accounted for an annual mean of 0.86 of total (public + private) bear harvests (SE=0.108) in 1998-2013 (Figure 1.5). I accordingly inflated Downing estimates from public lands by the annual ratio of public: total harvest, to derive abundance for Oconee county. I estimated an increasing trend in the abundance of black bears in Oconee county from a mean of 12.5 bears in 1998, to 158.9 bears in 2013 (Figure 1.3). This corresponded to a net increase of 12.7x in abundance over 15 years. I estimated a correspondingly increasing trend in density, from 0.04 bears/km² in 1998 to 0.32 bears/km² in 2013 (Figure 1.4), with a mean population growth rate of 1.11 per annum (SE=0.24). I excluded the year 1999 as an outlier in reporting population growth rate, with a point estimate of 2.57, attributed to unusually low hunting success (and correspondingly abundance) in 1999 (Figure 1.2).

I estimated average age of male bears harvested in Oconee county as 3.56 years (SE=1.86; Table 1.2). The 5 male bears harvested in Oconee in 1992-1995 were ≥ 8 years; however in 1996-2015 the average age of harvested male bears remained relatively constant in a range of 2 – 4.5 years (Mean = 3.67 years (SE=0.69)). I estimated average age of female bears in harvest as 3.6 years (SE=1.86; Table 1.2). However, I noted a breakpoint in trend at 2009; in 1997-2009 average age of harvested females was 2.86 years (SE=1.62), in 2010-2015 average age increased to 5.12 years (SE=1.13). I found sex ratios in Oconee county harvest biased in favor of males (Mean F: M ratio = 0.53 (SE=0.34); Table 1.2). Exceptions were 2005 and 2014, when females comprised ~55% and ~61% of the harvest respectively.

Pickens county. — In Pickens county, I found that public harvest accounted for an overall annual mean of 0.81 of total (public + private) bear harvests (SE=0.15) in 1999-2013 (Figure 1.5). I accordingly inflated Downing estimates from public lands by the mean annual ratio to derive abundance for Pickens county. I estimated an increasing trend in the abundance of black bears in Pickens county from a mean of 78.5 bears in 1999, to 214.0 bears in 2013 (Figure 1.3). This corresponded to a net increase of 2.7x in abundance over 14 years. I estimated a correspondingly increasing trend in density, from 0.46 bears/km² in 1998, to 0.73 bears/km² in 2013 (Figure 1.4), with a mean population growth rate of 1.05 per annum (SE=0.14).

I estimated average age of male bears harvested in Pickens county as 3.81 years (SE=1.49; Table 1.2). I noted that average age of males harvested was higher and showed greater variance prior to 2006 (Mean = 4.34 years (SE=1.71) in 1992-2005, Mean = 2.99 years (SE=0.61) in 2006-2015). I estimated average age of female bears in harvest as 4.68 years (SE=1.07; Table 1.2). I found sex ratios in Pickens county harvest biased in favor of females (Mean F: M ratio = 1.52 (SE=0.87); Table 1.2).

Greenville county. — In Greenville county, I found that public harvest accounted for an overall annual mean of 0.57 of total (public + private) bear harvests (SE=0.27) in 1998-2013 (Figure 1.5). I noted a sharp breakpoint in trend away from WMA harvest towards private harvest in 2009 (Mean WMA harvests: total harvest = 0.75 (SE=0.17) in 1998-2008, Mean WMA harvests: total harvest = 0.29 (SE=0.08) in 2009-2013). I accordingly inflated Downing estimates from public lands by the mean annual ratio to derive abundance for Greenville county. I estimated an increasing trend in the abundance

of black bears in Greenville county from a mean of 27.5 bears in 1999, to 89.8 bears in 2013 (Figure 1.3). This corresponded to a net increase of 3.3x in abundance over 15 years. I estimated an increasing trend in density, from 0.45 bears/km² in 1998, to 0.70 bears/km² in 2013 (Figure 1.4), with a mean population growth rate of 1.16 per annum (SE=0.57). I noted that population growth rates showed much higher variance in Greenville than Pickens and Oconee counties, as well as the entire northwest population.

I estimated average age of male bears harvested in Greenville county as 2.3 years (SE=0.84), with no significant change in trend over the period (Table 1.2). I estimated average age of female bears in harvest as 4.52 years (SE=2.48); Table 1.2). It should be noted that the greater observed variance in average age of females could be attributed to smaller sample size in harvest than for Oconee or Pickens counties. I found sex ratios in Greenville county harvest biased in favor of males (Mean F: M ratio = 0.73 (SE=0.91); Table 1.2).

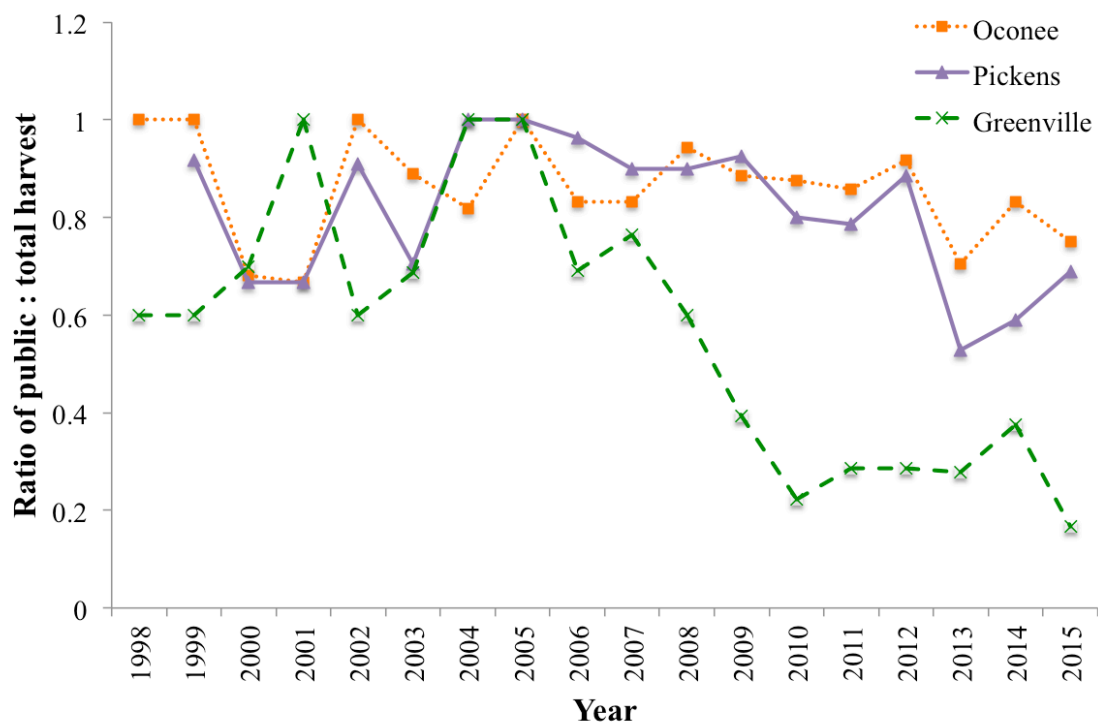


Figure 1.5. Percentage of black bear harvest on public (Wildlife Management Area) lands by county, in Game Zone 1, South Carolina, in 1998-2015.

Table 1.2. Average age (years) of males and females in harvest, and sex ratio (F: M) in harvest in 1992-2015, and mean and standard error (SE) over the entire period, for Oconee, Pickens, and Greenville counties in South Carolina.

Year	Oconee				Pickens				Greenville			
	Sample size	Average age (males)	Average age (females)	Sex ratio (F: M)	Sample Size	Average age (males)	Average age (females)	Sex ratio (F: M)	Sample size	Average age (males)	Average age (females)	Sex ratio (F: M)
1992	3	8.67	--	0.33	6	8.40	5.00	1.00	--	--	--	--
1993	--	--	--	--	--	--	--	--	--	--	--	--
1994	1	--	--	--	4	4.75	--	0.25	1	3.00	7.00	1.00
1995	3	9.00	--	0.33	8	3.00	5.33	3.00	1	--	3.00	--
1996	5	4.40	--	0.20	6	5.50	4.00	2.00	3	--	9.67	--
1997	7	--	2.00	0.60	8	--	--	0.60	5	--	--	0.67
1998	6	2.20	1.00	0.20	3	4.00	--	--	5	1.00	1.67	2.00
1999	3	3.00	1.00	0.50	11	4.33	3.67	2.00	4	2.33	4.00	0.33
2000	19	3.06	3.67	0.17	14	1.50	2.25	0.88	7	2.00	2.00	0.50
2001	3	3.50	2.00	0.50	14	4.50	4.70	2.00	4	3.50	--	0.25
2002	11	2.71	6.75	0.57	11	3.00	3.50	1.40	4	--	3.00	0.67
2003	16	2.17	4.40	0.89	26	3.42	4.14	0.59	14	2.00	10.38	0.78
2004	11	2.80	2.40	1.20	15	4.20	3.40	0.88	3	2.00	1.50	1.00
2005	8	2.17	1.00	0.14	9	5.50	5.86	4.00	7	1.00	5.00	0.14
2006	12	3.38	4.00	0.33	27	3.11	4.45	1.70	12	2.33	5.80	0.86
2007	23	4.47	3.00	0.28	20	3.75	5.71	2.33	15	2.00	3.38	3.00
2008	17	2.50	3.00	0.39	20	3.60	6.50	0.58	9	3.11	3.25	0.80
2009	31	2.45	2.90	0.67	40	3.73	3.80	1.29	20	3.92	3.80	0.33
2010	14	3.86	7.00	0.75	18	2.56	5.00	1.38	3	1.00	--	0.50
2011	23	2.97	4.92	0.55	48	2.50	5.22	1.07	9	2.00	4.80	0.71
2012	36	3.45	4.58	0.54	34	3.00	5.06	1.40	13	2.40	2.63	1.33
2013	43	3.39	5.67	0.61	48	3.30	5.53	1.30	36	3.06	5.08	0.68
2014	22	3.22	4.91	1.56	32	2.44	5.85	2.18	8	2.00	5.33	2.25
2015	40	3.79	3.64	0.43	28	2.00	4.94	1.64	24	3.87	3.20	0.33
Mean		3.67	3.57	0.53		3.81	4.68	1.52		2.27	4.52	0.91
SE		1.91	1.86	0.34		1.49	1.07	0.87		0.84	2.48	0.73

DISCUSSION

Populations of black bear in South Carolina appear to be increasing over the past two decades, although at a slower rate than previously estimated (Still 2007, Morton 2011). My data suggests that even discounting the ~100 bears estimate of the coastal population (Drewry 2010) and assuming a 15% underestimation by Downing reconstruction (Tilton 2005), the 2011 report of the northwestern SC bear population (Morton 2011) overestimated abundance by a factor of ~3. I attribute this to the original estimates being inaccurately derived from changes in sightings and harvest rather than a dedicated population survey. To validate my predicted abundance, I compared my results to non-spatial and spatially-explicit models used to analyze capture-recapture data from a hair-snare study in South Carolina in 2013-2014 (see Chapter 2). Point abundance estimates of the Downing method in 2013 (412.0 bears) agreed with both non-spatial (Model averaged mean=402.73, SE=109.67) and spatial models (Model averaged mean=360.70, SE= 51.53). This indicates that my Downing reconstruction technique was likely robust enough to predict long terms trends, and it is likely that fewer black bears persist in northwest South Carolina than previously reported.

Although the overall trend for the northwest population is increasing, trends at the county-level imply different stages of recovery for each of the black bear populations. Since harvest is the major source of mortality for hunted populations of black bear (Beecham 1983, Wooding and Hardisky 1994), I assumed that comparing the age- and sex- structures in harvest between areas with similar habitats and non-harvest mortality would provide insights into local flux in population dynamics. A number of studies report

greater male vulnerability to harvest for the species (McIlroy 1972, Fraser et al. 1982, Kohlmann et al. 1999, Malcolm and Van Deelen 2010), and postulate that a consistent male bias and relatively higher female average age in harvest indicates a lightly harvested population (Johnson and Pelton 1980, Fraser et al. 1982, Garshelis 1990, Garshelis 1994). In Oconee county, age and sex structures in harvest, along with high net population growth over the study period, and evidence of few individuals occupying the area in the early 1990s (Fendley 1991, Willey 1995) suggest that it is an expanding population which has not yet reached carrying capacity. In contrast, Pickens county abundance and density trends have flattened in recent years, suggesting that the population is either reaching carrying capacity or is being overharvested. Pickens also consistently reported a female bias in harvest over the study period. Although female bias in harvest is typically a sign of heavy exploitation, this could be attributed to an older population automatically having reduced male bias due to greater male vulnerability to harvest in younger age classes (Garshelis 1990). However, when combined with a relatively lower population growth rate and increased harvest in recent years (Figure 1.3; Figure 1.2) I suggest there is need for further research into the potential for overharvest in Pickens county.

In Greenville county, although black bear density in public lands oscillated greatly each year (Figure 1.4), abundance trends indicate a generally increasing population (Figure 1.3). Combined with the shift in trend to harvest of bears on private lands in recent years, I suggest this indicates that bears are expanding their geographic range and dispersing away from public forested lands. Moreover, deer-baiting with corn (which also attracts bears) has been permitted for South Carolina hunters since 2013 on

private, but not public lands (T. Wactor, pers. comm.). My hypothesis of dispersion is further supported by this recent opportunity to attract bears to private lands using deer-bait, the relative scarceness of public forested lands in Greenville county (Figure 1.1), and the generally increasing trend in bear-human interactions over the past decade (T. Wactor, pers. comm.; Figure 3.2(c)).

The Downing method has been proven robust to population trajectories over a long-term dataset (Downing 1980, Tilton 2005, Davis et al. 2007); however I recommend that it be considered a baseline estimate of point abundances each year. I suggest the future incorporation of hunting effort and/or harvest reporting rates to improve the robustness of the method. Simulation runs of the method have reported a tendency to underestimate point abundances by typically 11-15% but sometimes as high as 30% (Tilton 2005, Davis et al. 2007). However, this tendency was contradicted by point estimates for 2013 being similar to model averaged mean abundances reported from the 2013 capture-recapture study in the region (see Chapter 2). I recommend that these estimates be calibrated against future mark-recapture (or similar) surveys to better determine extent of underestimation. I also recommend that similar to this study, Downing trends for more recent years not be considered fully indicative of true abundance trends, as all animals in a cohort have not yet passed through the harvested population.

While increasing human densities have historically strongly corresponded with declining large mammal populations, implementation of effective legislation and management strategies can allow wild populations to expand even in regions of high

human densities (Kellert et al. 1996, Linnel et al. 2009, Treves and Karanth 2003). For the American black bear, the picture emerging over the past two decades in the eastern US is of bears repopulating former ranges, saturating the bear-human landscape, and state programs moving towards more informed management (Kellert 1994, Noyce 2011b). In South Carolina, a black bear population once declared probably extinct (Logan 1859), persisted to a few dozen individuals a century later amidst great public distrust, illegal kills, and increasing urban development (Cely and Hamilton 1981). A decade later, the population increased to about 100 individuals (Fendley 1991), and is currently steadily expanding over its former range while sustaining an annual recreational harvest. My findings indicate, however, that this recovery has been much slower than previously reported (as low as 1/3 below previous estimates), and varies at a county level. Therefore I suggest that, similar to multi-state large carnivore recovery programs decentralizing management efforts, there may be a need to vary management at a county-level (Carroll et al. 2006, Sandström et al. 2009, Linnel et al. 2010). Further, I suggest further investigation using projection models to understand how ecological factors and harvest management decisions at both state and county levels can maintain black bear recovery in the state for both desired levels of annual recreational harvest as well as minimization of bear-human conflict.

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CHAPTER TWO

APPLYING NON-SPATIAL AND SPATIALLY EXPLICIT CAPTURE-RECAPTURE
MODELS TO A SOUTH CAROLINA BLACK BEAR POPULATION

INTRODUCTION

Assessments of large carnivore populations are typically conducted indirectly, as their elusive or itinerant natures and large home ranges render it difficult to implement a direct count. A popular method of abundance or density estimation is the capture-recapture technique, wherein a population is repeatedly sampled, individuals are marked before release, and statistical models applied to the ‘capture history’ of detected individuals to estimate population-level metrics of interest (e.g., capture probabilities, abundance, population growth rate; White et al. 1982). Over time, biologists and wildlife managers have improved field techniques of capture and marking, with the multiple (and often concurrent) aims of non-intrusiveness, decreased cost or sampling effort, increased sample size, and collecting additional variables of interest such as age or location. The variety of techniques used to sample animal populations in a capture-recapture study include live-trapping (Willey 1995, Shanker 2000), aerial surveys (Bartmann et al. 1987, Fewster and Pople 2008), camera-trapping (Karanth 1995, Trolle and Kery 2003, Gerber et al. 2012, Noss et al. 2012), oral biomarkers (Garshelis and Noyce 2006, Peacock et al. 2011), and hair collection (Mowat and Paetkau 2002, Boulanger et al. 2004, Gardner et al. 2010) and scat surveys for genetic profiling (Ruell et al. 2009, Goode et al. 2014).

With readily available computer programs to analyze data, the past few decades have seen the development of increasingly sophisticated capture-recapture models to monitor parameters of abundance, density, sex ratios, and capture probabilities for effective wildlife management (Garshelis and Noyce 2006, Noss et al. 2012, Rayan et al. 2012, Junek et al. 2015). As abundance and density estimates are a crucial component of management and conservation actions, it is important that the statistical models used to draw inferences on the population are unbiased. Historically, maximum likelihood estimators (first described by Fisher 1922) of a parameter have been used in capture history analysis to estimate abundance (N), as they are typically consistent, normally distributed, and asymptotically unbiased, making them useful for statistical inference (Cooch and White 2006). However, density (D) is often of more intrinsic value than abundance to biologists studying the species, and is calculated by dividing N by the effective trapping area (A) of the sampled population. However, A is difficult to define and measure accurately as sampling grids for wide-ranging species typically cover only a subset of their entire geographic range (Efford 2004, Obbard et al. 2010). At least some individuals will have home ranges extending beyond the sampling grid, positively biasing D (White et al. 1982, Boulanger and McLellan 2001, Obbard et al. 2010, Gerber et al. 2012). Further, trap layouts do not necessarily represent population variation in space use (Hernandez-Blanco et al. 2013, Wilton et al. 2014), and any immigration to or emigration from the trapping area violate assumptions of demographic closure in closed capture-recapture models (Gerber et al. 2012).

Spatially explicit capture-recapture models were developed by Efford (2004) as a way to directly estimate density from capture histories without assuming geographic closure or effective area. His method combines a distance-dependent detection probability function with the spatially referenced locations of trap sites. By assuming that capture events are Poisson processes in time, the method establishes a spatial point process of home range centroids, the intensity of which is a direct estimator of density (Efford 2004). Spatially explicit capture-recapture models may be implemented using the traditional maximum likelihood estimation (Borchers and Efford 2008), Monte Carlo simulation and inverse prediction (Efford 2004), or in a Bayesian framework using Markov Chain Monte Carlo simulations (Royle and Young 2008). The advantages associated with spatially explicit models are well documented and include inherent accommodation of spatial heterogeneity in response to detectors and accommodation of non-uniform sampling designs in space (Efford 2004, Efford et al. 2009, Borchers 2010, Gerber et al. 2012, Efford and Fewster 2013, Efford and Mowat 2014). Although spatially explicit models are more computationally intensive than conventional closed capture and telemetry based estimators, tests against simulated data have shown the former to be generally less biased and robust to low capture probabilities and deviations from a Poisson distribution of home range centers (Sollman et al. 2011, Ivan et al. 2013, Gerber et al. 2012, Efford and Fewster 2013, Junek et al. 2015).

In this study I applied a maximum likelihood closed non-spatial capture-recapture method, and spatially explicit capture-recapture method to estimate density of a black bear (*Ursus americanus*) population in northwestern South Carolina. Specifically, my

objectives were to (1) compare density estimates produced by estimates of abundance from non-spatial models and an estimate of effective sampling area, to density estimates from spatially explicit models, and (2) to assess the assumptions and possible sources of bias in these models in order to make recommendations for the study design and analysis of future capture-recapture surveys of black bear populations.

METHODS

Study area

My study area included about 2200 km² in northwestern South Carolina across the counties of Oconee, Pickens, and Greenville. South Carolina Department of Natural Resources (SCDNR) personnel sampled black bear hair within grid cells using barbed-wire hair snares as described by Woods et al. (1999). In May 2013 a sampling grid of 5.8 km² squares was defined across the area. Size of cells in the sampling grid was based on a previously estimated black bear density of 1 individual per 5.8 km² (Settlage et al. 2008). Grid squares for hair snare sampling sites were either located within the core occupied area by black bear in northwestern South Carolina designated by SCDNR as South Carolina Game Zone 1, or they were located on forested lands owned or leased by SCDNR, South Carolina Department of Parks, Recreation & Tourism (SCPRT), United States Forest Service, Nature Conservancy, Natural Land Trust, and the D&M Hunt Club (T. Wactor, SCDNR, pers. comm.).

Site placement of hair snares within a grid square was determined by accessibility, and endeavored at a relatively uniform spacing between adjacent sites

(Figure 2.1). Average site spacing over the study area was 2.71 km. Site distribution within counties was as follows: 59 sites in Oconee, 28 sites in Pickens, and 28 sites in Greenville. The same hair snare site locations were used in both 2013 and 2014.

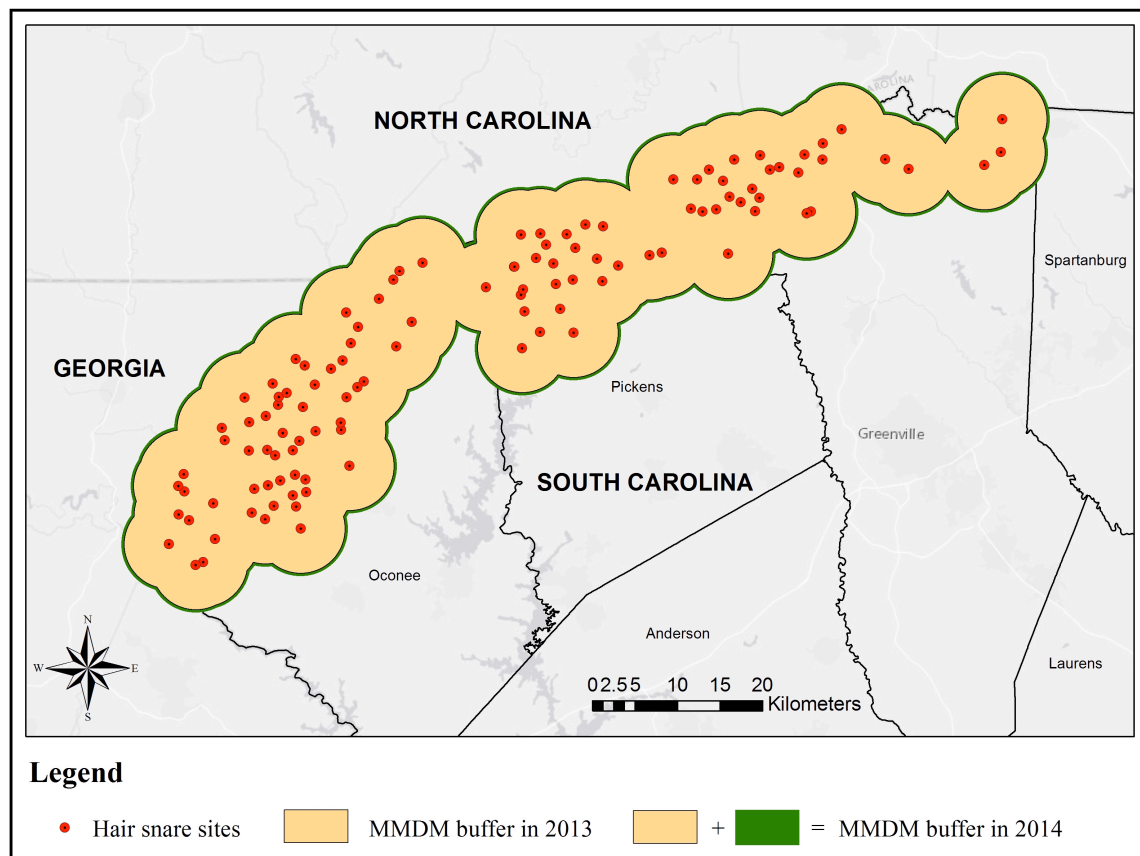


Figure 2.1. Location of hair snare sites for black bears, and area sampled with buffers based on mean maximum distance moved (MMDM) in northwestern South Carolina, 2013-2014. MMDM = 5.24 km in 2013 and 5.58 km in 2014.

Data collection

A barbed wire hair snare was established at each of the 115 sampling sites to collect black bear hair samples for individual identification. Hair snares were constructed with specifications described by Woods et al. (1999), where a hair snare or corral consisted of 2 strands of barbed wire stretched between 3-5 trees spaced at least 2.0 – 2.5 m apart on a flat surface. Wires were strung at 35 and 70 cm above ground, and sardines/bakery products as bait and scent lure (Mother Murphy's Raspberry Flavoring) was hung in the center of the corral approximately 1.5 – 2.0 m above ground. Beginning late May, snares were checked weekly for 8 weeks in 2013 and 7 weeks in 2014. Samples were gathered using tweezers sterilized between individual collections, with a propane torch to burn off remnant hair from the barbed wire before rebaiting.

SCDNR sent hair samples to Wildlife Genetics International (WGI), Canada for genotyping. Due to financial constraints, only a subset of the samples each year was budgeted for DNA analysis. In 2013, funds were allocated to analyze ~55% of the 650 hair samples collected. After technicians at WGI discarded samples that were inconsistent with bear hair under a microscope, or that contained inadequate material for sampling (minimum 1 guard hair root, or 5 underfur; D. Paetkau, WGI, pers. comm.), 584 samples remained. The subselection criteria established was as follows: One sample chosen from a single week-site combination with ≤ 3 samples, 2 samples from a single week-site with 4-6 samples, and 3 samples from a single week-site with ≥ 7 samples. In 2014, funds were allocated to analyze ~42% of the 843 hair samples collected. After WGI technicians discarded samples based on quality and appearance, 768 samples remained. A more

conservative subselection criteria was developed to increase the proportion of samples analyzed, compared with the 2013 protocol. In 2014, one sample was randomly chosen from a single week-site with ≤ 2 samples, 2 samples from a single week-site with 3-5 samples, and 3 samples from a single week-site with ≥ 6 samples.

DNA was extracted from hair samples using QIAGEN DNeasy Blood and Tissue kits (Qiagen, Valencia, CA), following standard protocols (Paetkau 2003, Roon et al. 2005). Individual analysis was carried out using 7 microsatellite markers (G1A, G1D, G10L, G10C, G10M, G10P, MU23) and 1 sex marker (ZFX/ZFY), selected from Settlage et al. (2008). The samples underwent three phases of analysis. First, an initial pass of identification where samples having high confidence scores were separated. Second, a cleanup phase where data points incomplete or difficult to read were repeatedly reanalyzed and samples that still had low confidence scores in any of the 8 markers were discarded. Genotype scores were classified using a combination of objective (peak height) and subjective (appearance) criteria; low confidence was identified by a 2-digit rather than a 3-digit score (D. Paetkau, pers. comm.). Third, an error-checking phase in which mismatching markers in a pair of genotypes were extended to 11 microsatellite loci to confirm that it was the same bear and not a genotyping error (D. Paetkau, pers. comm.).

Statistical Analysis

Non-spatial analysis. — I used individuals identified in the genetic analysis to create capture histories to estimate abundance using closed capture estimators in Program

MARK (ver. 8.0, www.phidot.org/software/mark). Capture histories were defined as a set of 1s and 0s for each individual, one number allotted per week, where 1 represented an individual visiting a site that week compared to 0 if it did not. White et al. (1982) separate the assumptions of population closure into demographic closure (i.e. no permanent births, deaths, immigration or emigration over the study period) and geographic closure (individuals do not move on and off the study area over the study period). I assumed a capture season of 7 or 8 weeks would not violate demographic closure for bears (Mowat and Strobeck 2000), and verified this using the *closure.test()* function in *secr* (Otis et al. 1978). Further, I used a buffer based on the Mean Maximum Distance Moved (MMDM) to minimize violation of geographic closure. As there were no individual covariates other than sex (e.g. morphological measurements) in my data, I used a full likelihood over conditional likelihood model in MARK. Assumptions of the full likelihood model were that every individual had equal probability of capture in a hair snare, or that capture probability varied depending on model parameters, e.g. sex, week of first capture, etc. (Williams et al. 2002). Detection parameters were capture probability (p), recapture probability (c), and a 2-mixture probability (pi) to account for individual heterogeneity. I fit a null model with no covariates and 16 models with varying effects on the detection parameters p , pi and c . Effects modeled included sex (g), temporal variation (t), and trap-response behavioral effects (b) that determined if an individual was likely to revisit or avoid a snare after having being captured once (Appendix B). Abundance N was estimated as a derived parameter separately for each sex. I ranked my models using Akaike Information Criterion corrected for small samples (AICc) and performed model

averaging using the Akaike weight ($AICc_w$) of competing models, where competing models were defined as $\Delta AICc \leq 10$ (Burnham and Anderson 2003).

I estimated density from N by calculating an effective area for the dataset equal to the study sites buffered by the mean maximum distance moved (MMDM) by individuals captured >1 time (Obbard et al. 2010, Sharma et al. 2010). Traditionally, $\frac{1}{2}$ MMDM was used as a site buffer (Dice 1938, Otis et al. 1978). More recently, when compared with telemetry data or spatially explicit models, MMDM has been shown to often outperform $\frac{1}{2}$ MMDM for studies with imperfect detection due to large trap spacing or low population densities (Soisalo and Cavalcanti 2006, Dillon and Kelly 2008, Obbard et al. 2009, Sharma et al. 2010).

Spatially explicit analysis. — I used the same set of capture histories used in my non-spatial analysis to estimate density using the maximum-likelihood based spatially explicit capture-recapture software package *secr* in R (ver. 2.10.3, <http://cran.r-project.org/package=secr>). I modeled data assuming individuals had stationary activity centers (i.e. no permanent immigration or emigration) using the following model arguments: (1) I modeled home range centers as a Poisson distribution assuming random homogenous distribution of individuals across the study area, since bears are not gregarious and exhibit mutual avoidance within overlapping ranges (Obbard et al. 2010), and (2) I modeled detection as a half-normal function assuming that detection was a continuous (not step) function from the home range centers to a point of zero capture probability (Borchers and Efford 2008, Goode et al. 2014). Detection parameters for models were probability of individual detection at the home range center (g_0), and rate of

decrease in capture probability with distance from home range center (σ). I fit a null model with no covariates and 8 models with varying effects on the detection parameters g_0 and σ . Effects included temporal variation (t), linear trend over sampling occasions (T), global trap response (b), and site-specific trap response (bk); where trap response behavior determined if an individual was likely to revisit or avoid a snare after having being captured once. Two point mixture distributions were used to model individual heterogeneity ($h2$) using sex as a covariate (Appendix B). Density (D) was estimated as a derived parameter, and $h2$ considered a sex ratio. I initially provided an approximate buffer of 6000 m to initialize the model, as derived from MMDM estimates rounded to the nearest km; however models reported a maximization [buffer] error. I corrected the approximate buffer to the value returned from the *suggest.buffer()* function in *secr*, rounded to the nearest km (7000 m in 2013, 6000 m in 2014). I ranked my models using Akaike Information Criterion corrected for small samples (AICc) and performed model averaging using AICc_w of competing models, where competing models were defined as $\Delta AICc \leq 10$ (Burnham and Anderson 2003).

RESULTS

Genetic analysis

Year 1 (2013). — The elimination and technical protocols resulted in 298/650 samples analyzed. Microsatellite analysis of the 298 samples revealed 143 individual bears (76M: 67F, M: F ratio of 0.53: 0.47). The genotyping success rate for individual identification was 89%. The 143 individuals were detected at 83.48% (96 of 115 sites) of

the hair snare sites in 2013. Fifty-nine individuals, or 41.26% of captures were in Oconee county (at 44 of 59 sites), 45 individuals or 31.47% of captures were in Pickens county (at 25 of 28 sites), and 40 individuals or 27.97% of captures were in Greenville county (at 27 of 28 sites).

Year 2 (2014). — The elimination and technical protocols resulted in 396/838 samples analyzed. Microsatellite analysis of the 396 samples revealed 149 individual bears (59M: 90F, M: F ratio of 0.4: 0.6) detected in 2014. Fifty-one of 149 (23M: 28F) were recaptures from 2013, whereas 98 (36M: 62F) were new individuals. The genotyping success rate in 2014 was lower than in 2013, with successful individual identification achieved for 77% of all samples genotyped in 2014. When data was reviewed by week, we noted unusually poor success rates for weeks 3 and 4 (59% and 71% respectively; D. Paetkau, pers. Comm.). When the success rate of individual identification was recalculated excluding weeks 3 and 4, it increased to 81%, which was more consistent with the 2013 results. The 149 individuals were detected at 80.86% (93 of 115 sites) of the hair snare sites in 2014. Sixty five individuals, or 43.62% of captures were in Oconee county (at 46 of 59 sites), 49 individuals or 32.89% of captures were in Pickens county (at 23 of 28 sites), and 36 individuals or 24.16% of captures were in Greenville county (at 24 of 28 sites). Of the 51 recaptures from 2013, 25 were from in Oconee (49.0%), 16 were from Pickens (31.4%), and 12 were from Greenville (19.6%) counties. Two individuals in the dataset were captured in > 1 counties. The first was in Pickens in 2013 and Oconee in 2014 (approximate distance between sites = 23.9 km); and the second in Greenville in 2013 and both Pickens and Greenville in 2014 (1 capture

in Pickens in Week 3, captures in Greenville in Weeks 1-6; approximate distance between sites = 49.5 km). The latter individual was excluded as an outlier from spatial models.

No individuals sampled were found in common between my dataset and any other projects analyzed by WGI for North Carolina, Georgia, Tennessee, and Florida. No individuals were found in common with my dataset and the 2004 Southern Appalachian study (Settlage et al. 2008) that included South Carolina.

Non-spatial analysis

Year 1 (2013). — My top-ranked model was Mth2 (individual heterogeneity and time as covariates of capture probabilities, and the 2-mixture probability was time invariant; Table 2.1; see Appendix B for a list of all models run). The model-averaged estimate of black bear abundance in 2013 was 214.07 males (SE=115.83) and 188.66 females (SE=102.28), for a total abundance of 402.73 bears (SE = 109.67; Table 2.1). The M: F ratio in this analysis was 0.53: 0.47. Mean capture probability over 8 weeks was identical for males and females (Mean = 0.079, SE = 0.046). Mean recapture probability over 7 weeks was 0.077 for males (SE = 0.041) and 0.132 for females (SE = 0.043).

I established an effective trap area as 2147.01 km² using an MMDM value of 5.24 km. I divided the abundance estimates by this effective area, and derived an ad hoc density estimate of 0.099 bears/km² (SE = 0.053 bears/km²) for males and 0.088

bears/km² (SE = 0.047 bears/km²) for females, giving a total mean density of 0.187 bears/km² (SE = 0.071 bears/km²).

Year 2 (2014). — My top model was Mb (trap response as a covariate for capture and recapture probabilities; Table 2.1; see Appendix B for a list of all models run). I eliminated models incorporating heterogeneity within a sex from results, as model averaged abundance estimates were ~1.75x that of 2013 (Mean = 694.46, SE = 222.72). After elimination and using model averaging, I derived an abundance estimate of 135.77 males (SE=71.53) and 217.60 females (SE=103.81), for a total abundance of 353.37 bears (SE = 92.75) (Table 2.1). The M: F ratio in this analysis was 0.38: 0.62. Mean capture probability over 7 weeks was nearly identical for males (Mean = 0.077, SE = 0.052), and females (Mean = 0.075, SE = 0.045). Mean recapture probability over 6 weeks was 0.281 for males (SE = 0.038) and 0.242 for females (SE = 0.028).

I established an effective trap area of 2255.96 km² using an MMDM value of 5.58 km. I divided the abundance estimates by this effective area, and derived an ad hoc density estimate of 0.060 bears/km² for males (SE = 0.032 bears/km²) and 0.096 bears/km² for females (SE = 0.046 bears/km²), giving a total mean density of 0.156 bears/km² (SE = 0.056 bears/km²).

Table 2.1. Abundance (N) and standard error (SE) of the non-spatial maximum-likelihood capture-recapture analysis with closed capture estimators in Program MARK. $AICc$ is Akaike's Information Criterion adjusted for small samples, $AICc_w$ is relative $AICc$ support for models, $h2$ is an estimator that accounts for individual heterogeneity, b is an estimator that accounts for behavioral bias, and t is an estimator that accounts for temporal variation. Competing models defined as $\Delta AICc \leq 10$.

Model	N	SE	AICc	$\Delta AICc$	$AICc_w$	# Parameters
Top models from 2013						
Mth2	390.43	94.37	181.82	0.00	0.7274	12
Mtbh2	435.53	141.36	183.78	1.96	0.2726	13
g*Mth2	395.35	141.58	197.74	15.93	0.0000	22
Top models from 2014						
Mb	354.57	77.96	122.32	0.00	0.5060	6
g*Mb	354.76	106.20	126.00	3.69	0.4832	10
Mtb	265.54	64.13	130.10	7.79	0.0069	11
Mt	180.04	5.37	131.46	9.14	0.0039	12
g*Mt	181.53	6.67	137.77	15.46	0.0000	5

Spatially explicit analysis

Year 1 (2013). — I found no evidence of violation of demographic closure assumptions from the *closure.test()* function results ($z = -1.96$, $P = 0.03$). Initialized buffer size around traps was 6.49 km, returned by the program based on individual movement, however this increased to ~8 km for several models run. My top model ($g_0 \sim h_2 + bk + T$, $\sigma \sim h_2$) included sex, site-specific trap response, and linear trend as covariates for g_0 , and sex as a covariate for σ (Table 2.2; see Appendix B for a list of all models run). I derived a model averaged density estimate of 0.168 bears/km² (SE=0.024) with a M: F ratio of 0.36: 0.64. This resulted in estimates of 0.060 bears/km² for males and 0.108 bears/km² for females.

We multiplied the mean density estimate by an effective study area of 2147.01 km² calculated using MMDM, and derived an ad hoc abundance estimate of 360.70 bears (SE=51.53), with a male/female distribution of 128.82 and 231.88 bears respectively.

Year 2 (2014). — I found no evidence of violation of demographic closure assumptions from the *closure.test()* function ($z = -1.81$, $P = 0.04$). Initialized buffer size around traps was 5.57 km, returned by the program based on individual movement; however this increased to ~7 km for several models run. My top model ($g_0 \sim h_2 + bk$, $\sigma \sim h_2$) included sex and site-specific trap response as covariates for g_0 , and sex as a covariate for σ (Table 2.2; see Appendix B for a list of all models run). I derived a model averaged density estimate from this model of 0.177 bears/km² (SE=0.023) with a M: F ratio of 0.25: 0.75. This resulted in estimates of 0.044 bears/km² for males and 0.133 bears/km² for females.

We multiplied the mean density estimate by an effective study area of 2255.96 calculated using MMDM, and derived an ad hoc abundance estimate of 399.30 bears (SE=51.89), with a male/female distribution of 99.26 bears and 300.04 bears respectively.

Table 2.2. Density (D) and standard error (SE) for top models of the spatially-explicit maximum-likelihood capture-recapture analysis using package *secr* in R. $AICc$ is Akaike's Information Criterion adjusted for small samples, $AICw$ is relative $AICc$ support for models, $g0$ is the probability of detection at home range center, σ is rate of decrease in detection with distance from home range center, $h2$ is an estimator that accounts for sex-specific heterogeneity, b is an estimator that accounts for behavioral bias, and bk is an estimator that accounts for site-specific bias. Competing models defined as $\Delta AICc \leq 10$.

Model	Density (bears/km ²)	SE	AICc	$\Delta AICc$	AICc _w	# Parameters
Top models from 2013						
$g0 \sim h2 + bk + T, \sigma \sim h2$	0.168	0.024	2139.81	0.00	0.6698	8
$g0 \sim h2 + bk + T, \sigma \sim h2 + T$	0.167	0.024	2141.54	1.73	0.2816	9
$g0 \sim h2 + bk, \sigma \sim h2$	0.170	0.025	2145.05	5.25	0.0486	7
$g0 \sim h2 + bk + t, \sigma \sim h2$	0.168	0.024	2150.18	10.37	0.0000	14
Top models from 2014						
$g0 \sim h2 + bk, \sigma \sim h2$	0.178	0.023	2243.15	0.00	0.4794	7
$g0 \sim h2 + bk + T, \sigma \sim h2$	0.176	0.023	2243.63	0.48	0.3776	8
$g0 \sim h2 + bk + T, \sigma \sim h2 + T$	0.175	0.022	2245.65	2.50	0.1377	9
$g0 \sim h2 + bk + t, \sigma \sim h2$	0.176	0.023	2252.16	9.01	0.0053	13
$g0 \sim h2 + bk, \sigma \sim 1$	0.161	0.020	2257.69	14.54	0.0000	6

DISCUSSION

My study provides novel insights into black bear densities in northwestern South Carolina, and highlights the potential for model choice to influence density estimates. My ad hoc density estimates from the 2013 closed capture models (0.188 bears/km²) were higher than spatially explicit models (0.168 bears/km²). However, my ad hoc density estimates from closed capture models in 2014 (0.156 bears/km²) were lower than spatially explicit models (0.177 bears/km²), but nearly doubled when individual heterogeneity within sex was incorporated. This discrepancy in results is consistent with other studies that report higher ad hoc density estimates from non-spatial models when compared to spatially explicit models (Soisalo and Cavalcanti 2006, Dillon and Kelly 2008), and can probably be attributed to a violation of the assumption of geographic closure (Efford 2004). I found support for the hypothesis of geographic closure violation from the buffer size around snare sites (used to calculate effective study area and subsequently density) being greater in spatially explicit models than non-spatial models. I observed that there was considerable variation in estimates of density among different models fitted to the same dataset in *secr*, particularly when individual heterogeneity was incorporated in the model. This demonstrates the potential for *secr* to predict biased estimates when an inappropriate model is fit. A number of studies (Proctor et al. 2010, Ebert et al. 2010, Howe et al. 2013) suggest that density estimates are conservative for models that do not incorporate heterogeneity, although Howe et al. (2013) recommend incorporating other parameters along with heterogeneity to avoid over-inflation of density.

My estimates of black bear density from both MARK and *secr* models were lower than that of a 2004 mark-recapture study (0.233-0.456 bears/km²) reported for the population (Settlage et al. 2008). However I noted that the Settlage et al. (2008) study only overlapped with a part of my study region (Pickens Ranger District of the Sumter National Forest in South Carolina), and moreover also included samples from black bear populations in National Forest lands of Georgia and North Carolina. Although I established 24.3% of all hair snare sites in Pickens county, I detected 31-33% of individuals each year on those sites. Compared to Oconee (51.4% of sites and 41-44% of detected individuals) and Greenville (24.3% of sites and 24-28% of detected individuals) counties; this suggests that Pickens has a higher density of bears than Oconee and Greenville.

My results reported a few differences in behavior and sex ratios in 2013 and 2014. In 2014, recapture success for females was nearly twice that of 2013, and recapture success for males nearly four times that of 2013. However in 2014, I analyzed 98 more samples with approximately the same number of individuals detected, which might account for the difference in recapture ratios. Further, while M: F ratios in samples in 2013 and 2014 were reflected in the MARK models, M: F ratios were biased towards females in the *secr* models in both years. However, as *secr* estimates sex ratios from a stationary distribution of activity centers, whereas sex distribution in the sample is influenced by differential movement and capture probability by sexes, I suggest that the sex ratios returned by spatial models are more likely a true representation of the sex ratios in the population.

A potential source of underestimation of density in *secr* models is the assumption that all bears have equal movement across the landscape. However, most study areas will include unavailable habitat stemming from topographic barriers and anthropogenic features (Rayan et al. 2012). In future investigations, I recommend surveying expanded areas that could be defined as historically unoccupied or unsuitable bear habitat. Once sampled, these habitat covariates or geographical coordinates could be used in the habitat mask feature of *secr* to exclude non-habitat areas, improve density estimates, and reduce probable underestimation in future surveys.

Density is an important parameter in population ecology studies, and often a crucial component of conservation or wildlife management actions. For a harvested species such as the black bear, inflated estimates can lead to management plans that put the population at risk (Gardner et al. 2009, Obbard et al. 2010, Sollman et al. 2011, Gerber et al. 2012, Noss et al. 2012). My findings indicate that spatially explicit capture-recapture models reflect an annual variation in density that is more consistent with the biology and management of the black bear population than non-spatial capture-recapture models. I suggest that the density estimates from this study be used as a baseline for biologists as they review current management of the population.

Overall, I recommend using spatially explicit capture recapture models over the MMDM approach, regardless of grid size. Even when combined with telemetry data, density from N/A has been reported as an overestimation (Soisalo and Cavalcanti 2006, Dillon and Kelly 2008), as the estimate of A does not necessarily account for all home range sizes. Further, when density is derived from N/A , although naïve standard errors for

density are reported from standard errors of N , A is typically a point estimate. This assumes that A is measured with no uncertainty, which overstates the precision of the density estimate (Obbard et al. 2010). The *secr* program, on the other hand, warns when initialized buffer values are not large enough to meet internal mathematical assumptions about movement from the data, and recommends alternate buffer sizes. Spatially explicit capture-recapture models, which assume no permanent immigration or emigration (Efford 2004), are generally more suitable when there is uncertainty about study design effectiveness, either due to itinerant nature or underestimated home ranges of the species.

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CHAPTER THREE

INFLUENCE OF ACORN MAST ON BLACK BEAR POPULATION GROWTH
RATES AND HUMAN-BEAR INTERACTIONS IN NORTHWESTERN SOUTH
CAROLINA

INTRODUCTION

A number of ecosystems are characterized by pulsed resources, which consist of periodic events of high resource availability followed by long inter-pulse events of reduced resource availability. Some well known examples include periodic outbreaks of insects (Hahus and Smith 1990, Yang 2004), increased plant growth following an El Nino event (Wright et al. 1999, Stapp and Polis 2003), seasonal transfer of nutrients from oceans to riparian systems by migrating salmon (Helfield and Naiman 2001), and mast fruiting by trees (Sork et al. 1993, Kelly 1994). Masting is defined as a synchronous highly variable seed production among years by a large population of plants (Kelly 1994). Plants appear to track abiotic environmental variations to induce masting (Norton and Kelly 1988, Wright et al. 1999), and evolutionary benefits facilitated by masting include satiating predators to enable lower percentage of seeds consumed than in non-masting years, which in turn facilitates pollination (Kelly 1994, Isagi et al. 1997, Ostfield and Keesing 2000).

As mast fruits are an irregular resource, it is expected that the consumers most likely to respond to a masting event are trophic generalists (Ostfeld and Keesing 2000). In deciduous forest ecosystems, masting events can cause rapid population growth in

generalists such as white-footed mice (*Peromyscus leucopus*; Elkinton 1996, Ostfeld et al. 1996, McShea 2000), eastern chipmunks (*Tamias striatus*; Wolff 1996, McShea 2000), and white-tailed deer (*Odocoileus virginianus*; McShea and Schwede 1993), with growth rates declining in interpulse intervals. The American black bear (*Ursus americanus*) is also a generalist consumer, with a diet comprised generally of acorns, berries, grasses, insects, small rodents, birds, carrion, and also foods from anthropogenic sources (Beeman and Pelton 1980). In the Southern Appalachian region, they appear to prefer extensive, mature hardwood forests with late successional nut (acorn (*Quercus* spp.), hickory (*Carya* spp.), hazelnut (*Corylus* spp.)) and berry (blueberry (*Vaccinium* spp.), huckleberry (*Gaylussacia* spp.), service berry (*Amelanchier* spp.)) trees (Pelton 1986, Landers et al. 1997). However, acorns in particular represent the primary, energy-rich source of food and hibernation reserves for bears in the Appalachians during the dormant season (Beeman and Pelton 1980, Garner 1986, Clark 2004). Pelton (1989) reports that bears in the Appalachians may respond to mast failure by undertaking long-range movements, or intensively using small areas of high acorn concentration. Subsequently, this change in activity may lead to increased animal-human conflict (Ryan et al. 2004, Sato and Endo 2006, Ryan et al. 2007, Baruch-Mordo et al. 2014, Obbard et al. 2014). Hard mast failure may also negatively impact female age of reproductive maturity, litter size, and barrenness, suggesting that population growth may subsequently fluctuate with success of mast crops (Jonkel and Cowan 1971, Beeman and Pelton 1980, Eagle and Pelton 1980, Eiler et al. 1989, McLean and Pelton 1994, Costello et al. 2003).

The direct correlation of masting to black bear population growth rates has been less well-established. While studies have documented the influence of mast on seasonal movement and activity (Beeman and Pelton 1980, Schooley et al. 1994, Kozakai et al. 2013), reproductive potential (Jonkel and Cowan 1971, Rogers 1976, Eiler et al. 1989, Costello et al. 2003, Jakubas et al. 2005), mortality and human interactions (Beeman and Pelton 1980, Ryan et al. 2004, Ryan et al. 2007, LaMere 2012, Obbard et al. 2014), and bait station visitation (Clark et al. 2005), few studies have assessed the relationship between production of acorn mast and population growth rates using long term datasets (McLean and Pelton 1994, Clark et al. 2005, Reynolds-Hogland et al. 2007). In South Carolina, black bears are managed as a game species, and it is thus important for wildlife managers to understand the factors that affect their population growth rates, and human-bear interactions. However, no study had been carried out in the state relating population dynamics to acorn mast.

In this study, I used a 15-year dataset of black bear abundance derived from harvest (see Chapter 1) and long-term mast records from the South Carolina Department of Natural Resources (SCDNR) to examine the effect of acorn masting events on the population growth rates (λ) of black bear and human-bear interactions in northwestern South Carolina. Specifically, I hypothesized that a time-lagged, positive correlation exists between acorn mast indices and λ . Bear populations were predicted to increase ≥ 2 years after large mast events, considering recruitment of cubs born next spring to the harvestable population at ages ≥ 1 . I also hypothesized a negative correlation between acorn mast indices and human-bear interactions, likely due to increased foraging activity

by bears in years of mast failure. Finally, bait station indices (the percentage of sardine bait stations visited by bears) are used as a population index for bears in South Carolina, but their efficacy had not been examined against λ , and Garshelis (1990) suggested visitation could vary with physiological and environmental covariates including food resource availability. Accordingly, I hypothesized a positive correlation between visitation to bait stations and λ , and predicted that visitation would be impacted positively by a diminished availability of mast.

METHODS

Study area

My study area primarily consisted of the region where bear harvest was permitted in northwestern South Carolina, characterized by the SCDNR as ‘Game Zone 1’ that extends over Oconee, Pickens, and Greenville counties (Figure 3.1). Forest types in this region generally consisted of shortleaf pine (*Pinus echinata*), chestnut oak (*Quercus prinus*), scarlet oak (*Q. coccinea*) and hickory (*Carya sp.*) mixes on the southern Appalachian slopes (Willey 1995, Butfiloski 1996). Other notable masting species found in the region included white oak (*Q. alba*), post oak (*Q. stellata*), Northern red oak (*Q. rubra*), Southern red oak (*Q. falcata*). Biotic and climatic conditions were generally similar across all forested lands in the counties under consideration. For the response variables of human-bear interactions and non-hunting mortality, I also considered in my dataset conflict and roadkill reports from the counties of Anderson, Spartanburg, Laurens, and Cherokee that surrounded the primary study area.

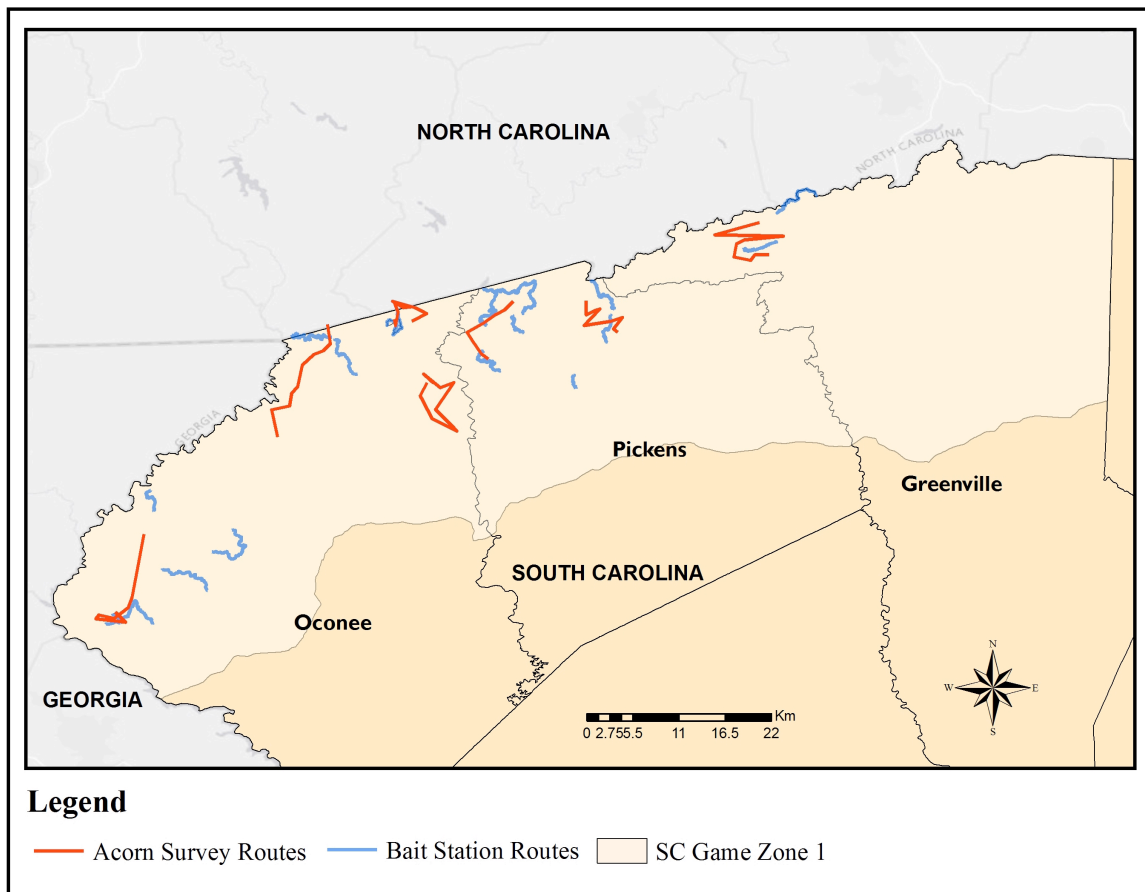


Figure 3.1. Location of acorn mast survey and bait station routes, and the South Carolina Department of Natural Resources defined Game Zone 1 for black bear harvest in the northwest region.

Data collection

Hard mast index (HMI). — I used 23 years of hard mast survey data collected by SCDNR, from 1993 – 2015. Surveys were conducted annually between August 15 and September 15 in established bear habitat, and survey routes were established such that altitudes varied as much as possible (Greenberg 2007; Figure 3.1). Routes were at least 16 km, with stops at 1.6 km intervals, and 2 – 4 tagged trees of each oak group were surveyed at each stop (new trees selected only if previously tagged trees were dead or logged, in the same vicinity and having dimensions similar to the old tree; Greenberg 2007). Oak groups consisted of species preferred for consumption by black bears, grouped into the following categories: 1) “White oak” – white oak (*Q. alba*) and post oak (*Q. stellata*), 2) “Red oak” – Northern red oak (*Q. rubra*), Southern red oak (*Q. falcata*), black oak (*Q. velutina*), and scarlet oak (*Q. coccinea*), 3) Chestnut oak (*Q. prinus*), and 4) Hickory (*Carya sp.*). Hickory data was only collected from 2004 onwards.

At each selected tree, acorn crops were rated on a relative scale using a hard-mast index (HMI). From 1993 to 2005, SCDNR personnel adapted the Whitehead (1969) survey method. This included for each tree a scored estimate of the percentage of tree crown with acorns (PCA), and counts of twigs, twigs bearing acorns, and number of acorns on a random subsample of 5 oak limbs >90 cm long. From 2006 to 2015, SCDNR personnel used the Greenberg (2007) survey method that was standardized across the Southern Appalachian Black Bear Study Group (SABBSG 2007). This method estimated PCA by a surveyor looking up at the tree crown for 30 seconds, and proportion of trees

bearing acorns (PBA) was then calculated as percentage of all trees sampled with PCA >35%. A regression equation was used to determine the HMI as:

$$y = b_0 + b_1x$$

where y was the predicted HMI, x was PBA and b_0 and b_1 were regression equation coefficients specific to the species of oak (Greenberg 2007). The Greenberg method was developed to predict the Whitehead method HMI using a less labor intensive technique. I interpreted HMI of mast crop for each tree group as: 0.0-2.0 = Poor, 2.1-4.0 = Fair, 4.1-6.0 = Good, and 6.1-8.0 = Excellent (Greenberg 2007).

Black bear data. — I used 18 years of annual harvest records maintained by the SCDNR to reconstruct black bear populations in northwestern South Carolina (see Chapter 1). Techniques are described in detail in Chapter 1, but essentially consisted of utilizing age- and sex- specific records of each harvested bear to reconstruct the population. I augmented the dataset with non-harvest mortality, which consisted of road kill and euthanized nuisance bears. Due to scarce data prior to 1998 and the limitations of the technique to reconstruct recent years, I reconstructed abundance for 1998 – 2013 only.

I also generated an annual index of human-bear interactions (HBI) from 2004 – 2015 based on nuisance bear reports submitted to SCDNR, typically contacted as the first responders to human-animal conflict in the region. This included visual sightings, property invasions, and crop damage by black bear.

Bait station index (BSI). — I used 23 years of bait station visitation data from 1993 – 2015, collected by the SCDNR as part of a multi-state initiative to indicate

changes in population (Clark et al. 2005). Bait station surveys were conducted between July 15 – August 10, annually from 1993 – 2005, and from 2005 – 2015 they were conducted every 2 years (i.e., odd years). Bait station transects, or bait lines, were established in accordance with Carlock et al. (1983) guidelines, and consisted of 10 stations spaced at 0.8 km intervals (Figure 3.1). At each station, a partially-opened can of sardines was suspended 2.5 – 3.0 m above ground level in a tree 10 – 20 cm in diameter, left for 5 nights, and then inspected for black bear visitation (Fendley 1991). Visitation was a presence-absence index determined by one or more of the following signs: tracks, bent/broken trees, claw marks on trees and tooth punctures in sardine cans (Fendley 1991). BSI was calculated as percentage of bait stations visited by bears.

Bait station surveys were divided into core and fringe areas. The core area was defined as traditional bear habitat based on harvest and nuisance records that consisted of properties in the Jocassee Gorge in eastern Oconee and northern Pickens Counties, and the Camp Greenville area in northern Greenville County. The fringe area consisted of areas west of Lake Jocassee in Oconee County and the remaining bear inhabited areas of Pickens and Greenville Counties (SCDNR website).

Statistical Analysis

I corrected for time-varying processes in all datasets by converting time series data to percentage or rate change in annual values. I calculated the annual population growth rate (λ) over the study period using the formula $\lambda = N_t/N_{t+1}$. I converted BSI into ΔBSI using the formula $\Delta BSI_t = BSI_t - BSI_{t-1}$. I used the R package *forecast* (ver 7.1,

<http://github.com/robjhyndman/forecast>) to check datasets for need for further autoregression with the *acf* (autocorrelation) function, which is based on the standard Pearson's correlation coefficient (r) applied to a time series with a lag, and the *auto.arima* function to identify autoregressive transformations if any. I computed pairwise associations between each category of HMI (white oak, red oak, chestnut oak, hickory) and λ , Δ BSI, and HBI, using the function *ccf* to check for cross-correlation with a lag of upto 3 years. I chose a 0 to 3-year lag, considering that mast quality in year_t could affect reproductive potential of females in year_t, subsequent birth of cubs in year_{t+1}, and recruitment into the harvestable population in year_{t+2} (McLean and Pelton 1994, Clark et al. 2005). I also computed pairwise time-lagged cross-correlations between Δ BSI and λ . When carrying out cross-correlations I trimmed datasets to match years of the shortest dataset.

I then built a set of regression models with λ and HBI as response variables using a bottom-up approach by adding statistically significant correlations, defined as $|r| > 0.40$ (Evans and Over 1996), as dependent variables. For response variable λ I considered all permutations of white oak, red oak, chestnut oak and Δ BSI as dependent variables, and also applied 0 to 3 year time-lagged effects for each dependent variable. For response variable HBI, I considered all permutations of white oak, red oak, and chestnut oak. I only included a 0 to 1 year time lagged effect for HBI, assuming that human interactions and road kills would not be affected by > 1 year previous mast production.

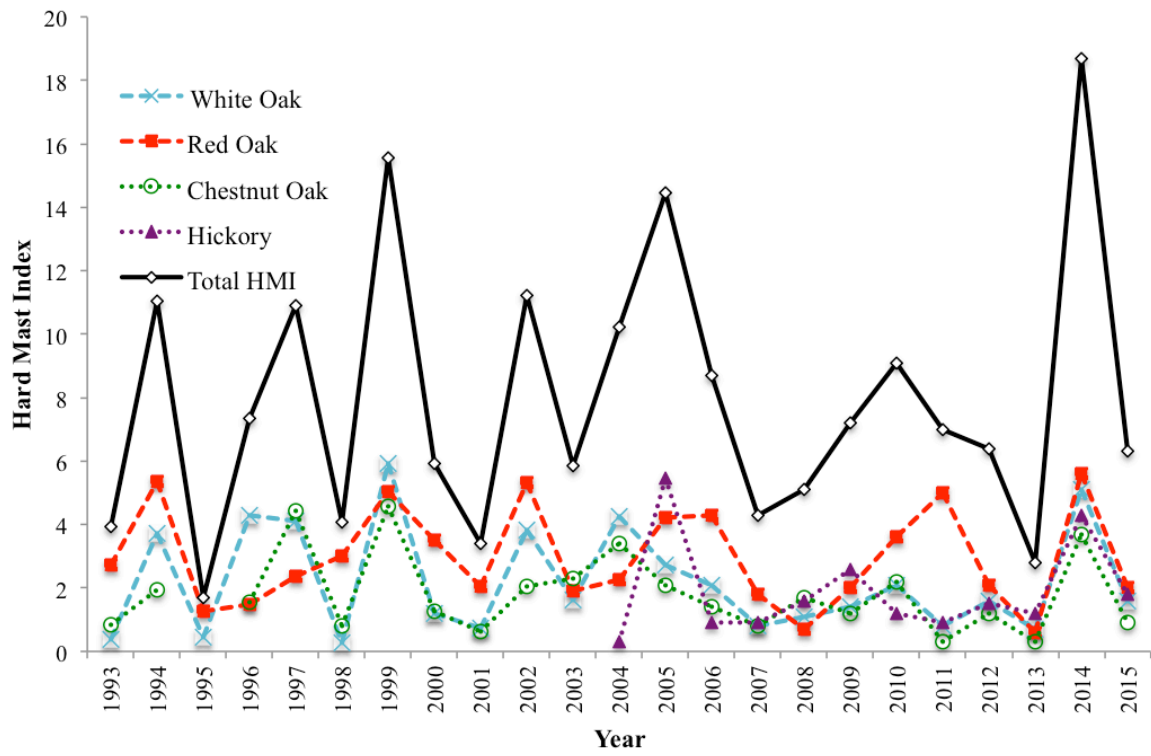
After running all permutations of dependent variables, I eliminated statistically significant ($P < 0.1$) regression models having R^2 values < 0.5 . I also eliminated additive

models (>1 covariate) where the addition of one covariate removed statistical support ($P < 0.1$) for all others. I compared the remaining models using Akaike's Information Criterion corrected for small samples (AICc) to determine relative statistical support. Note that I did not model average, as is recommended when the primary goal is variable selection rather than parameter prediction (Arnold 2010).

RESULTS

Total HMI fluctuated from year to year with consecutive peaks recurring every 2-3 years, except for a period in 2004 – 2010 that had 6 years between peaks (Figure 3.2(a)). Based on visual assessment, white oak had consecutive peaks recurring approximately every 2-3 years, red oak every 3-5 years, chestnut oak every 2-5 years, and hickory every 2-4 years (Figure 3.2(a)). Red, white, and chestnut oaks also showed an overall decline in mast production in 2004 – 2010. λ and HBI fluctuated with consecutive peaks recurring every 2-4 years, and BSI_{core} as well as BSI_{fringe} showed a generally increasing trend over the study period (Figure 3.2(b); 3.2(c); 3.2(d)).

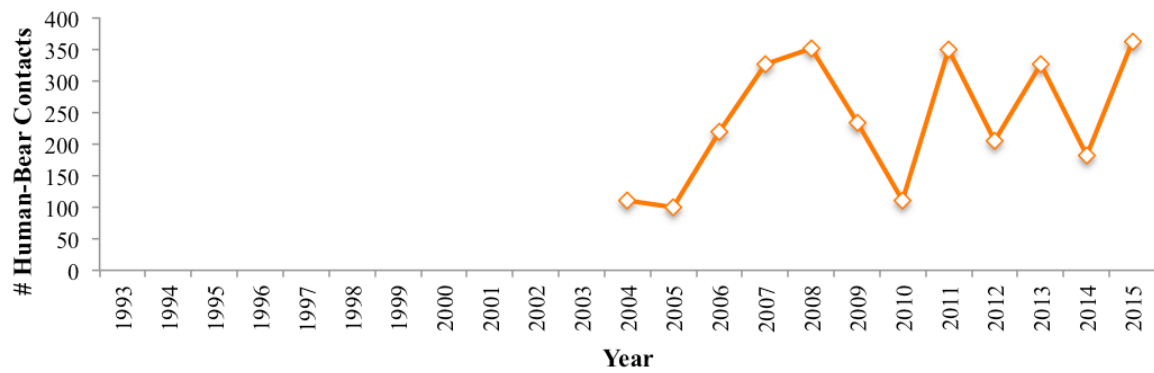
(a)



(b)



(c)



(d)

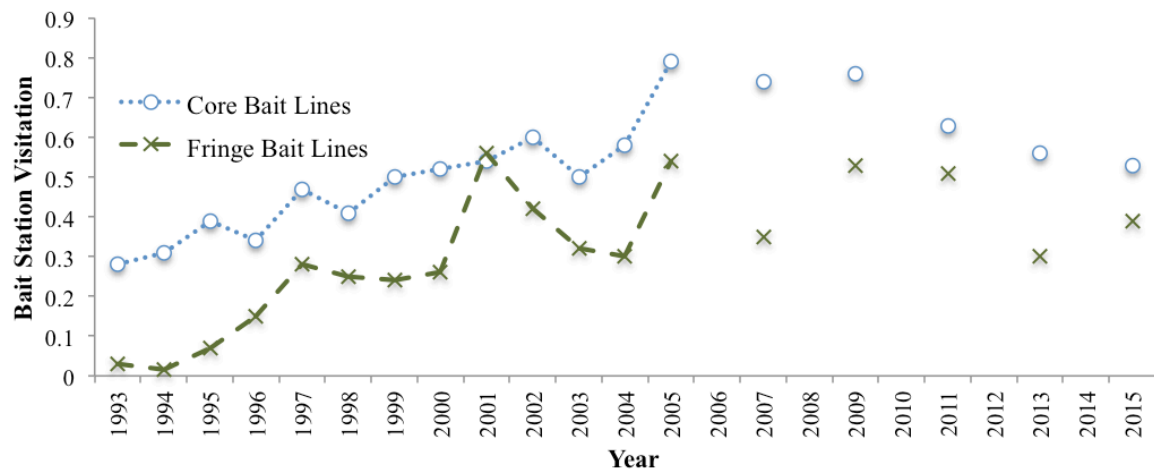


Figure 3.2. Time series plots of (a) hard mast index (HMI), (b) population growth rate of black bears (λ), (c) number of human-bear contacts, and (d) percentage bait station visitation by bears in northwestern South Carolina in 1993 – 2015.

Population growth. — There was no significant autocorrelation ($|r| > 0.40$), or need for autoregression, in the λ time series as well as HMI time series of all oak groups (both individually and combined; Table 3.1). Pairwise cross-correlation checks revealed moderate correlation between λ and white oak at a 0 and 2 year time lag ($r = 0.486$ and 0.47 respectively), chestnut oak at a 0 year time lag ($r = 0.441$), and $\Delta\text{BSI}_{\text{core}}$ at a 0 year time lag ($r = 0.438$), and strong correlation between λ and red oak at a 1 year time lag ($r = 0.704$) (Table 3.1). My top regression model predicting λ at year t was white oak with a 2 year time-lag + red oak with a 1 year time lag ($R^2 = 0.652$, $P < 0.001$, $\text{AICc}_w = 0.357$) (Table 3.2). However the next two models were also supported from AICc results (Table 3.2). The second best model included white oak with a 0 year time lag and the third included chestnut oak with a 0 year time lag; in addition to the two covariates of the top model. White oak and chestnut oak had a moderate positive relationship to the population growth rate of black bears, whereas red oak had a strong inverse relationship to the growth rate.

Table 3.1. Matrix depicting autocorrelations and cross-correlations between lambda, hard mast indices for various oak species, bait station indices (BSI), and human-bear interactions (HBI). Variable_A vs Variable_A represents a significant ($|r| > 0.40$) autocorrelation. Variable_A vs Variable_B represents a significant ($|r| > 0.40$) cross-correlation with Variable_B lagging Variable_A by time ($t-n$) years. + or – are used to show positive or negative cross-correlations

	Lambda	White oak	Red oak	Chestnut oak	Hickory	ΔBSI_{core}	ΔBSI_{fringe}	HBI
Lambda	--	+0.486 _(t) , +0.47 _(t-2)	-0.704 _(t-1)	+0.441 _(t)	--	+0.438 _(t)	--	--
White oak		--						
Red oak			--					
Chestnut oak				--				
Hickory					--			
ΔBSI_{core}	+0.441 _(t)	--	--	+0.463 _(t)	--	--		
ΔBSI_{fringe}	--	--	--	--	--		--	
HBI		-0.688 _(t)	-0.415 _(t)	-0.721 _(t)	--	--	--	--

Table 3.2. Covariates of the top regression models predicting population growth rate (λ) for black bears in northwestern South Carolina in 1998 – 2013. AIC_c is Akaike’s Information Criterion adjusted for small samples, AIC_{c_w} is relative AIC_c support for models, and df is degrees of freedom in the model. + or – before a covariate indicate positive or negative regression slope.

Model covariates	Covariate coefficient	Covariate p-value	df	AIC_c	ΔAIC_c	AIC_{c_w}	R-squared
White oak(t-2)	0.035	0.014	4	-26.20	0.00	0.357	0.65
Red oak(t-1)	-0.063	0.001					
White oak(t)	0.024	0.074	5	-26.09	0.11	0.339	0.72
White oak(t-2)	0.032	0.013					
Red oak(t-1)	-0.057	0.001					
White oak(t-2)	0.033	0.012	5	-25.58	0.62	0.263	0.71
Red oak(t-1)	-0.058	0.001					
Chestnut oak(t)	0.031	0.092					
White oak(t)	0.028	0.099	4	-25.87	4.33	0.041	0.54
Red oak(t-1)	-0.057	0.006					

Human bear interactions. — There was no significant autocorrelation ($|r| > 0.40$) or need for autoregression in the HBI time series (Table 3.1). Pairwise cross correlation checks revealed moderate correlation between HBI and red oak at a 0 year time lag ($r = -0.415$), and strong correlation between HBI and white oak at a 0 year time lag ($r = -0.688$), and chestnut oak at a 0 year time lag ($r = -0.721$) (Table 3.1). My top model predicting HBI at year t was white oak at a 0 year time lag ($R^2 = 0.67$, $P < 0.05$, $AICc_w = 0.567$), and white oak had a strong inverse relationship to λ (Table 3.3). Competing models from AICc rankings included total HMI across all species and chestnut oak as covariates, and both had an inverse relationship to human-bear interactions.

Table 3.3. Covariates of the top regression models predicting human-bear interactions for black bears in northwestern South Carolina in 2004 – 2015. *AICc* is Akaike’s Information Criterion adjusted for small samples, *AICc_w* is relative *AICc* support for models, and *df* is degrees of freedom in the model. + or – before a covariate indicate positive or negative regression slope.

Model covariates	Covariate coefficient	Covariate p-value	df	AICc	$\Delta AICc$	AICc _w	R-squared
–White oak(t)	-77.88	0.002	3	115.26	0.00	0.567	0.67
–Total HMI(t)	-30.64	0.004	3	116.58	1.31	0.295	0.62
–Chestnut oak(t)	-84.69	0.008	3	118.09	2.82	0.138	0.56

Bait station indices. — Bait station indices were autoregressed, indicating that black bear visitation for year (t) was dependent on year ($t-1$). Using the *auto.arima()* function I received an ARIMA(0,1,0) value for the BSI_{core} and BSI_{fringe} time, indicating that using BSI_t as a dependent variable required the additive inclusion of BSI_{t-1} to correct for autoregression. However I found no significant autocorrelation ($|r| > 0.40$) or need for autoregression in the ΔBSI time series. ΔBSI values were only available until 2005 as BSI was collected every alternate year after 2005. Pairwise cross-correlation checks revealed moderate correlation between ΔBSI_{core} and lambda at a 0 year time lag ($r = 0.438$) and chestnut oak at a 0 year time lag ($r = 0.581$) (Table 3.1). However, all statistically significant ($P < 0.1$) regression models could not sufficiently predict lambda from visitation indices (i.e., model R^2 values were < 0.5).

DISCUSSION

My results supported the hypothesis that population growth rate of black bears in South Carolina was linked with the quantity of acorn mast crop in the region, although this relation varied with oak species. A positive 2-year time lagged relation to white oak supported the biological hypothesis that female bears reared cubs with greater success of survival during a good mast year (Eiler et al. 1989, Pelton 1989), which when weaned 2 years later were represented in the harvested population that I used to derive abundance. However I did not have corresponding survival data from dedicated studies on cub survival rates in the SC population to confirm this hypothesis. In contrast to white oak mast production, the population also showed a significant negative correlation, with a 1

year lag, to red oak mast. Clark (2004) reports that due to red oak acorns being more unpalatable from higher tannin content; black bears as whole acorn consumers prefer white oak acorns. Furthermore, I lacked sufficient data to judge the role of secondary food sources to moderate the effect of acorn mast. Availability of soft mast is hypothesized to offset the impact of hard mast failure on population growth for black bears in the Southern Appalachians (Garshelis and Pelton 1981, Eiler et al. 1989, Pelton 1989, Reynolds-Hogland et al. 2007), and it is likely that a future collection and inclusion of these data would improve the predictive power of my models.

It is generally agreed upon that resource limitation drives survival and recruitment, and eventually population growth rates of animals (Rogers 1987, McLean and Pelton 1994, Sinclair and Krebs 2002, Costello et al. 2003). However, these species-system ecological relationships are complex, and with trophic generalists such as the black bear, it may be especially difficult to pinpoint a few factors that primarily drive population growth. My study suggests that while acorn mast may act as a predictor for population growth, it is certainly not the only contributing factor. My results suggest that white oak might impact population growth by increase in foraging activity and associated mortality in poor mast years. However, other studies emphasize the relationship of mast to reproductive success, suggesting that acorn mast regulates females' health and ability to nurse a cub over winter until soft mast production in spring (Eiler et al. 1989, McLean and Pelton 1994). I postulate that the availability of other data such as movement, foraging activity periods, time of torpor retreat, and female fecundity and cub survival

rates would present a more complete picture of how both hard and soft mast impact the expansion and growth of the population.

The number of human-bear interactions were negatively correlated with acorn mast in the same year, which supported the biological hypothesis that bears increase foraging range and activity to meet nutritional needs during years of mast failure (Rogers 1987, Pelton 1989, Healy et al. 1997). This suggests that, similar to previous studies, black bears in this study area are less likely to forage near human settlements or scavenge personal property during good mast years, likely indicating an avoidance of human dominated landscapes when natural food is available (Peine 2001, Baruch-Mordo et al. 2014). However, some studies have shown that variation in natural food does not explain variation in HBI when bear populations are 1) expanding their range, or 2) urban development and recreation is expanding into bear habitat, or 3) bears become habituated to unnatural (human) food sources (Singer and Bratton 1980, McCarthy and Seavoy 1994, Schirokauer and Boyd 1998, Peine 2001, Cotton 2008, Obbard et al. 2014). Given the evidence from harvest records that the SC bear population is expanding both numerically and geographically (see Chapter 1), I thus recommend that agencies monitor mast-conflict correlations for signs of increasing interactions with no corresponding change in mast. Such signs may signify a need for increased conflict mitigation training of wildlife personnel and public educational programs. Furthermore, I recommend future spatio-temporal assessments of human-bear encounters as a potential index of change in habitat use and geographical spread of bears in the state.

Although bait station indices have been generally considered an indication of density since first established by Carlock et al. (1983), my results did not support a significant relationship between the bait station indices and population growth rate. Further, bait station indices showed no significant correlation to acorn mast, and a relative shift from core to fringe bait stations showed no correlation to increased bear-human interactions. Pelton (1989) suggests that visitation may be affected by one individual visiting multiple stations, or merely portray bears' use of trails used to set up bait lines (LeCount 1982). It is important to note that the precedent Carlock et al. (1983) study that established the technique used bait stations as pre-baits for trap sites in their mark-recapture study and thus visitation and capture rates used to predict abundance were not independent (Pelton 1989). Other studies linking BSI to abundance or population growth rates have been inconclusive or negative (Johnson 1989, Garshelis 1990, Clark et al. 2005), and Rice et al. (2001) suggested that statistical power required to detect long-term trends in visitation rates is not typically met by wildlife agencies' survey effort. Although intuitively bait station indices may represent changes in population, I likely lacked the required sample size as well as either supporting covariates or the spatial/temporal scales to determine the relationship (Clark et al. 2005). I suggest the need for state wildlife agencies to reevaluate the utility of using bait station visitation as a population index, particularly where resources are insufficient to 1) survey at appropriate scales and 2) validate results against more robust population estimates.

While state wildlife agencies regularly collect annual environmental data or population indices, these data might not translate into rigorous scientific assessment of

the relationship of these data to population management techniques (Garshelis 1990, Clark et al. 2005, Garshelis and Hristienko 2006, Reynolds-Hogland et al. 2007, Howe et al. 2010). With a long-lived and elusive species such as the black bear, the impact of any demographic or environmental stochasticity might not be apparent to a wildlife agency until several years after the population has responded to the event (Pelton 1989, Garshelis 1990, McLean and Pelton 1994, Noyce and Garshelis 1997, Brongo et al. 2005, Garshelis and Hristienko 2006). My study was a preliminary investigation into a few factors of the complex species-system interaction of South Carolina black bear. My results reflect on the gaps in current monitoring practices and provide ideas towards refining them. Finally, I stress on the need for dedicated scientific studies that validate these monitoring practices and develop standardized robust predictive models of how populations respond to environmental and anthropological events. Ultimately, this information can help agencies manipulate growth by regulating harvest for game species or managing habitat, or resolve conflict by predicting and preparing personnel for increased activity in specific areas (Peine 2001, Hristienko and McDonald 2007, Reynolds-Hogland et al. 2007, Baruch-Mordo et al. 2008, Obbard and Howe 2008, Obbard et al. 2014, Lewis et al. 2015).

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APPENDICES

Appendix A

Downing population reconstruction

The Downing (1980) reconstruction requires the following data: total harvest by year (aged + un-aged) (H_t), and sampled harvest-by-age in a year ($S_{a,t}$). The equations used in the reconstruction are as follows:

The first step is to calculate a ratio of aged to total harvest each year (A_t). Calculate a new corrected inflated harvest-by-age ($H_{a,t}$) by dividing $S_{a,t}$ by A_t . Collapse the older age classes to the desired age class (x) by summing $H_{a,t}$ for all ages $\geq x$.

The second step is to calculate a mean corrected harvest for an “average year”, which is created as a starting point by averaging the harvest of the 3 most recent years ($t = y, y - 1, y - 2$) over the 2 oldest age classes ($a = x, x - 1$), as

$$C_x = (H_{x,y} + H_{x,y-1} + H_{x,y-2})/3$$

and

$$C_{x-1} = (H_{x-1,y} + H_{x-1,y-1} + H_{x-1,y-2})/3$$

The third step is to calculate the average mortality rate of the 2 oldest age classes, as

$$M_x = C_{x-1}/(C_x + C_{x-1})$$

$$M_x = M_{x-1} = M$$

Estimate the total number of animals in the oldest age class at the “average year” t as

$$Z_x = C_x/M$$

Now we begin the population reconstruction at the most recent year (y) and work backwards through time. For the most recent year, the abundance for the 2 oldest age classes ($x, x-1$) is calculated as follows:

$$N_{x,y} = H_{x,y} / [1 - Z_x / (Z_x + H_{x-1,y} + H_{x,y})]$$

and

$$N_{x-1,y} = H_{x-1,y} / [1 - Z_x / (Z_x + H_{x-1,y} + H_{x,y})]$$

In other years, the abundance for the 2 oldest age classes is calculated as follows:

$$N_{x,t} = H_{x,t} / [1 - N_{x,t+1} / (N_{x,t+1} + H_{x-1,t} + H_{x,t})]$$

and

$$N_{x-1,t} = H_{x-1,t} / [1 - N_{x,t+1} / (N_{x,t+1} + H_{x-1,t} + H_{x,t})]$$

All younger age classes for all years are reconstructed using the equation:

$$N_{a,t} = N_{a+1,t+1} + H_{a,t}$$

Note that reconstructed abundance is incomplete for $(x - 1)$ years. For instance, collapsing to 4+ years produces incomplete age classes and thus underestimated population estimates for the most recent 3 years.

Appendix B

Capture-recapture models run

Table B.1. List of covariates used in non-spatial maximum-likelihood models analyzing black bear capture-recapture data in the South Carolina hair snare study in 2013-2014.

These include effects, or covariates, modeled on detection parameters p = capture probability, c = recapture probability, and p_i = a 2-mixture probability to account for individual heterogeneity.

Covariate	Description	Notes
g	sex	sex of the individual, here either ‘male’ or female’
t	time factor	step change in time, or secondary sampling occasion, here ‘week’
h2	individual heterogeneity	individual heterogeneity in capture probabilities
b	behavioral response	learned response to capture, or step change in capture probability after first capture

Table B.2. List of models run in the non-spatial analysis of black bear capture-recapture data in the South Carolina hair snare study in 2013-2014, to estimate detection parameters and abundance.

Model	Notes
M_0	capture and recapture probabilities are constant and time invariant; i.e. $p = c$
M_b	capture and recapture probabilities show behavioral response only, and capture probability of an unmarked individual \neq capture probability of a marked individual; i.e. p, c are estimated separately
M_t	capture probabilities show time response only; i.e. $p_i = c_i$ where $i = 1, 2, \dots K$, K = number of secondary sampling occasions
M_{h2}	divide individuals into 2 groups A and B , each group has relatively homogenous capture probabilities; i.e. $p_x = c_x$ where $x = \text{group } A \text{ or } B$, $p_i = \text{number of individuals in group } A$; number of individuals in group B , p_i is time invariant
M_{tb}	capture and recapture probabilities show both time and behavioral responses; i.e. p_i, c_i are estimated separately where $i = 1, 2, \dots K$
M_{th2}	capture probabilities show both time and individual heterogeneity responses; i.e. $p_{ix} = c_{ix}$, $i = 1, 2, \dots K$, $x = A \text{ or } B$, p_i is time invariant
M_{bh2}	capture and recapture probabilities show both behavioral and individual heterogeneity responses; i.e. p_x, c_x are estimated separately where $x = A \text{ or } B$, p_i is time invariant
M_{tbh2}	capture and recapture probabilities show time, behavioral, and individual heterogeneity responses; i.e. p_{ix}, c_{ix} are estimated separately, $i = 1, 2, \dots K$, $x = A \text{ or } B$, p_i is time invariant
g^*M_0	capture and recapture probabilities are constant and time invariant within a sex; i.e. $p_{males} = c_{males}$, estimated separately from $p_{females} = c_{females}$
g^*M_b	capture and recapture probabilities show behavioral response only, and differ for each sex
g^*M_t	capture probabilities show time response only, and differ for each sex
g^*M_{h2}	capture probabilities show individual heterogeneity, for 2 groups within each sex
g^*M_{tb}	capture and recapture probabilities show both time and behavioral responses, and differ for each sex
g^*M_{th2}	capture probabilities show both time and individual heterogeneity responses, and differ for each sex
g^*M_{bh2}	capture and recapture probabilities show both behavioral and individual heterogeneity responses, and differ for each sex
g^*M_{tbh2}	capture and recapture probabilities show time, behavioral, and individual heterogeneity responses, and differ for each sex

Table B.3. List of covariates used in spatially explicit maximum-likelihood models analyzing black bear capture-recapture data in the South Carolina hair snare study in 2013-2014. These include effects, or covariates, modeled on detection parameters $g0$ = the probability of detection when home range center is located at a snare, and σ = scale factor or rate of decrease in detection with distance from home range center.

Covariate	Description	Notes
t	time factor	step change in time, or secondary sampling occasion, here ‘week’
T	trend factor	linear trend in secondary sampling occasions, over a link scale
h2	individual heterogeneity	sex-based heterogeneity in capture probabilities, here either ‘male’ or ‘female’
b	global behavioral response	global learned response to capture, or step change in capture probability after first capture
bk	site-specific behavioral response	learned response to capture specific to the site of capture

Table B.2. List of models run in the spatial analysis of black bear capture-recapture data in the South Carolina hair snare study in 2013-2014, to estimate detection parameters and density.

Model	Notes
$g0 \sim 1, \sigma \sim 1$	the spatially explicit capture probability ($g0$) as well as the scale parameter (σ) are constant, or invariant across individuals, sexes, occasions, and snare sites
$g0 \sim h2, \sigma \sim 1$	$g0$ varies with sex (male or female), σ is constant
$g0 \sim h2, \sigma \sim h2$	both $g0$ and σ vary with sex
$g0 \sim h2+b, \sigma \sim 1$	$g0$ varies with sex; learned response to capture affects $g0$, similarly across all snare sites (globally)
$g0 \sim h2+b, \sigma \sim h2$	both $g0$ and σ vary with sex; learned response to capture affects $g0$ globally
$g0 \sim h2+bk, \sigma \sim 1$	$g0$ varies with sex; learned response to capture affects $g0$; differently depending on snare location (site-specifically)
$g0 \sim h2+bk, \sigma \sim h2$	both $g0$ and σ vary with sex; site-specific learned response to capture affects $g0$
$g0 \sim h2+t, \sigma \sim 1$	$g0$ varies with sex as well as secondary sampling occasion, σ is constant
$g0 \sim h2+t, \sigma \sim h2$	both $g0$ and σ vary with sex, $g0$ also varies with secondary sampling occasion
$g0 \sim h2+b+t, \sigma \sim 1$	$g0$ varies with sex as well as secondary sampling occasion, global learned response affects $g0$, σ is constant
$g0 \sim h2+b+t, \sigma \sim h2$	both $g0$ and σ vary with sex, both sampling occasion and global learned response affect $g0$
$g0 \sim h2+bk+t, \sigma \sim 1$	$g0$ varies with sex, both sampling occasion and site-specific learned response affect $g0$, σ is constant
$g0 \sim h2+bk+t, \sigma \sim h2$	both $g0$ and σ vary with sex, both sampling occasion and site-specific learned response affect $g0$
$g0 \sim h2+b+T, \sigma \sim 1$	$g0$ varies with sex, global learned response affects $g0$ which shows a trend over sampling occasions, σ is constant
$g0 \sim h2+b+T, \sigma \sim T$	$g0$ varies with sex, global learned response affects $g0$, both $g0$ and σ show a trend over occasions
$g0 \sim h2+b+T, \sigma \sim h2$	both $g0$ and σ vary with sex, global learned response affects $g0$ which shows a trend over occasions, σ is constant
$g0 \sim h2+b+T, \sigma \sim h2+T$	both $g0$ and σ vary with sex, global learned response affects $g0$, both $g0$ and σ show a trend over occasions
$g0 \sim h2+bk+T, \sigma \sim 1$	$g0$ varies with sex, site-specific learned response affects $g0$ which shows a trend over occasions, σ is constant
$g0 \sim h2+bk+T, \sigma \sim T$	$g0$ varies with sex, site-specific learned response affects $g0$, both $g0$ and σ show a trend over occasions
$g0 \sim h2+bk+T, \sigma \sim h2$	both $g0$ and σ vary with sex, site-specific learned response affects $g0$ which shows a trend over occasions, σ is constant
$g0 \sim h2+bk+T, \sigma \sim h2+T$	both $g0$ and σ vary with sex, site-specific learned response affects $g0$, both $g0$ and σ show a trend over occasions
$g0 \sim h2+bk+T, \sigma \sim h2+T$	both $g0$ and σ vary with sex, site-specific learned response affects both $g0$ and σ , which both show a trend over sampling occasions